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The Role of nannoplankton in the phytoplankton dynamics of four Colorado River reservoirs (Lakes Powell, Mead, Mohave, and Havasu)

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THE ROLE OF NANNOPLANKTON IN THE PHYTOPLANKTON DYNAMICS OF FOUR COLORADO RIVER RESERVOIRS (LAKES POWELL, MEAD, MOHAVE, AND HAVASU)

By

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ABSTRACT

Phytoplankton species composition and community size structure were studied in four warm-monomictic Colorado River reservoirs; lakes Powell, Mead, Mohave, and Havasu from March 1981 to February 1982. Sampling was done at approximately monthly intervals from several stations in each reservoir. The Utermöhl technique was used to enumerate phytoplankton. The phytoplankton assemblage was divided into the following six size classes using microscopic techniques; netplankton (>64 um), and nannoplankton (>5, 5-11, 12-21, 22-44, and 45-64 um).

Total phytoplankton biomass and community size structure were different among these four reservoirs with considerable spatial and temporal variation present. Average reservoir-wide areal weighted biomass was similar in lakes Powell, Mohave, and Havasu (0.8-0.9 g/m^3) while biomass in Lake Mead was lower (0.3 g/m^3). Based on maximum and mean annual phytoplankton biomass, all four reservoirs are classified as oligotrophic.

Highest station biomass was measured near the inflows; the Colorado River at Hite (Lake Powell), Eldorado Canyon (Lake Mohave), and upper Lake Havasu; the San Juan River at Zahn Bay (Lake Powell); and Las Vegas Wash at Middle Las Vegas Bay (Lake Mead).

Phytoplankton size structure was similar in lakes Powell and Mead where netplankton (>64 um) was the main component, contributing 37 and 42 percent of the total annual biomass, respectively. The

most common species in this size class were, *Synedra ulna* (Nitz.) Ehr., *Fragilaria crotonensis* (Edw.) Kitton, and *Ceratium hirundinella* (Mueller) Schrank. Nannoplankton were more common in lakes Mohave and Havasu where the 22-44 um size component made up 45 and 37 percent of total biomass, respectively. The most important species in this size class were *Cryptomonas erosa* Ehr., *Peridinium* spp., and *Anomoeoneis vitrea*.

Biomass of cells <21 um were also important in lakes Mohave and Havasu, contributing one third of total annual biomass. Several small flagellates were numerous in all four reservoirs. *Rhodomonas minuta* var. *nannoplanctica* Skuja, *Katablepharis ovalis* Skuja, and *Chrysochromulina parva* Lackey were observed in nearly every sample.

Nutrient levels were generally highest near the inflows, however, total phosphorus concentrations were low in all four reservoirs. Average values were 0.009 mg/l in Lake Powell, 0.011 mg/l in Lake Mead, and 0.012 mg/l in lakes Mohave and Havasu. Ortho-phosphorus (PO_4-P) was extremely low at all locations. Average concentrations ranged from 0.003 to 0.004 mg/l in each reservoir. Average total nitrogen concentrations were 0.429 mg/l in Lake Powell, 0.364 mg/l in Lake Mead, 0.346 mg/l in Lake Mohave, and 0.337 mg/l in Lake Havasu.

Physical characteristics are different among these reservoirs but most similar in Powell-Mead and Mohave-Havasu. The former two reservoirs are characterized by greater mean and maximum depth, surface area, volume, and longer hydraulic rentention time. Nutrients, inflow-outflow and physical characteristics appear to be most important in regulating the

phytoplankton biomass size structure and species composition in these reservoirs.

TABLE OF CONTENTS

LIST OF FIGURES

Figure		Page

LIST OF TABLES

INTRODUCTION

Size structure of phytoplankton communities is important in understanding community metabolism, nutrient uptake, photosynthesis and respiration. Size-dependent relationships have been shown for phytoplankton cell size and: biomass specific growth and reproduction rates (Williams 1964, Eppley and Sloan 1966), turnover rate (Nauwerck 1963), nutrient uptake (Smith and Kalff 1982, Dugdale 1967, Eppley et al. 1969, Laws 1975, Schlesinger et al. 1981), grazing (Burns 1968, Starkweather 1980, Bevan et al. 1978), sinking rate (Hutchinson 1967, Walsby and Renolds 1980), and decomposition (Pavoni 1963, Munawar and Munawar 1978).

Phytoplankton biomass in freshwater lakes spans a size range from small unicellular flagellates 1-2 um in diameter to large colonial and filamentous forms reaching several mm in length or breadth. The spectrum of sizes has generally been divided into two categories, nannoplankton and netplankton. Nannoplankton were originally defined as organisms not retained by the finest plankton nets, but could be obtained by centrifugation (Lohmann 1903, 1911). However, since the original description, the definition of nannoplankton has been refined to include those algae ranging from 20-100 um (Table 1).

Studies on natural lakes demonstrate that small phytoplankton cells (nannoplankton) are important components to total lake biomass as well

Table 1. Size classification of nannoplankton and netplankton as defined by various investigators.

Author	Nanno-	Net-	Location
	Plankton (um)		
Lohmann (1903,1911)	<25	>25	Marine
Cushing (1958)	5-60	>60	Sea
Rodhe et al. (1958)	<100	>100	Lake Erken, Sweden
Willen (1959)	<60	>60	Lake Malaren, Sweden
Strickland (1960)	10-50	50-500	Marine Phytoplankton
Pavoni (1963)	<30	>30	Zurich Lake
Hutchinson (1967)	5-60	>60	General
Gliwicz (1967)	>50	<50	Polish Lakes
Malone (1971)	<22	22-90	Eastern Pacific
Kristiansen (1971)	<50	>50	Danish Lakes
Kalff (1972)	<64	>64	Lake Hertel, Canada
Mommaerts (1973)	<50	>50	North Sea
Munawar et al. (1974)	<64	>64	Lake Ontario
Gelin (1975)	<20	>20	Lake Vombsjon, Sweden
Gelin and Ripl (1978)	<30*		Lake Trumen, Sweden
Munawar et al. 1978	<64	>64	Great Lakes

* Size fraction ingestable by zooplankton

as primary productivity. Nannoplankton tend to dominate in oligotrophic waters while netplankton increase in relative abundance as eutrophication increases (Kalff 1972, Pavoni 1963, Findenegg 1965).

The purpose of this study was to investigate phytoplankton biomass size structure in four reservoirs located on the Colorado River. Reservoirs are different from natural lakes in through-flow characteristics and depth of outflow (Neel 1963, Wright 1967). These reservoir systems are extremely important to the southwest, and are highly regulated to serve mutiple-use demands for power generation, recreation, and agriculture.

My objectives were to determine the phytoplankton biomass size structure and trophic relationships in lakes Powell, Mead, Mohave, and Havasu and to evaluate the factors influencing this size structure. To do this I evaluated the temporal and spatial biomass size structure based on biomass size fractions and mean equivalent spherical diameter (ESD). I also examined the role of nutrients, density currents, and inflows and outflows in affecting trophic status in lakes Powell, Mead, Mohave, and Havasu.

Previous studies have focused on the importance of nannoplankton to phytoplankton size structure. Of total phytoplankton biomass, Pavoni (1963) found that nannoplankton constituted between 6 and 9% in Lake Zurich, and 14% in the less eutrophic Lake Pfaffikon. Of total biomass, highest proportions of nannoplankton biomass (100%) were found in oligotrophic and hypertrophic waters, and lowest proportions (0-25%) in eutrophic waters. Pavoni considered the upper limit of nannoplankton to be 30 um but also included longer rod shaped or filamentous organisms

which could, depending on their orientation, pass through a 30 um net. Rodhe (1962) found most (97%) of the biomass consisted of nannoplankton in high mountain lakes of the Austrian Alps. Nannoplankton in the Swedish Lake Malaren accounted for nearly 40% of total phytoplankton volume (Willen 1959). Costella et al. (1979) reported that nannoplankton (3-54 um) contained 63% of all epilimnetic chlorophyll in oligotrophic Great Central Lake, British Columbia. Paerl (1977) found that ultraplankton (0.2-3 um) formed 11-35% of the biomass in oligotrophic and eutrophic New Zealand lakes. In Lake Hertel, a naturally eutrophic lake, Kalff (1972) found that nannoplankton (<64 um) contributed from 9 to 99% of monthly phytoplankton biomass. In extremely oligotrophic Lac Matamec, Canada, ultraplankton (<15 um) represented 47% of total phytoplankton biomass (Ross and Duthie 1981).

Munawar's studies on the Laurentian Great Lakes demonstate the importance of nannoplankton (<64 um) under a wide range of nutrient levels and trophic conditions. In oligotrophic Lake Superior, nannoplankton contributed from 57-80% of total annual biomass (Munawar et al. 1978). In Lake Erie, of total phytoplankton biomass, nannoplankton comprised a major portion of the biomass during spring and fall periods in trophic conditions which ranged from mesotrophic to eutrophic (Munawar and Munawar 1976).

Several studies reported the contribution of nannoplankton to phytoplankton productivity. Verduin (1957) reported that 60% percent of the measured photosynthetic activity from Lake Erie water passed through 64 um mesh net bolting cloth. Rodhe et al. (1958) found that rates of photosynthesis correlated more closely with nannoplankton numbers than

with phytoplankton cells retained in plankton nets. Findenegg (1965) found the highest photosynthetic activity (production/biomass) in periods with high relative frequencies of nannoplankton. High surface-to-volume ratios in nannoplankton allow for greater nutrient uptake rates and a relatively greater surface area exposed to light. Gelin (1975) found that nannoplankton had significantly greater photosynthetic capacity than netplankton. Gelin and Ripl (1978) reported that before the restoration of Lake Trummen, Sweden, 60% of primary productivity was contributed by phytoplankton cells passing through a 45 um plankton net. After restoration, total productivity decreased, with 85% contributed by algae passing through a 45 um net and 60% passing through a 10 um net. Munawar and Munawar (1982) found that the highest production/biomass ratios in the Laurentian Great Lakes usually occurred when nannoplankton and phytoflagellates dominated the community.

Two general conclusions result from studies in natural, mostly north-temperate zone lakes: (i) nannoplankton tend to dominate in oligotrophic waters while, with increasing trophic status, nannoplankton biomass increases but the relative (percentage) biomass decreases and (ii) temporal fluctuations in netplankton abundance and biomass are of greater magnitude than nannoplankton (Munawar and Munawar 1975, Renolds 1978).

Phytoplankton-Historical

Previous studies of Lake Powell phytoplankton have been limited to localized areas of the reservoir. Stewart (1974) and Stewart and Blinn

(1976) studied the environmental factors influencing phytoplankton success in Warm Creek Bay of lower Lake Powell. Hannsman et al. (1974) analyzed primary productivity to evaluate man's impact on eutrophication of the impoundment. Taylor et al. (1979) sampled one station during spring, summer, and fall of 1975 for the Environmental Protection Agency (EPA) National Eutrophication Survey. Czarnicki and Blinn (1977, 1978) provided excellent taxonomic keys to the diatoms of lower Lake Powell and the Grand Canyon. Information from these previous studies are difficult to compare with this study because phytoplankton biomass was not always reported, nor was there adequate attention given to phytoflagellates.

Studies of Lake Mead phytoplankton are equally rare. Since the first phytoplankton investigation of Lake Mead (Moffett 1943), most of the studies have been confined to Las Vegas Bay (Jonez and Sumner 1954, FWPCA 1967, Koenig et al. 1972, Deacon and Tew 1973, Baker et al. 1977). Staker et al. (1974) conducted the first lake-wide phytoplankton investigation. Many of these studies used membrane filters to concentrate the algal cells. Delicate nannoplankton are easily damaged or destroyed under filtration pressure or from improper preservation. As a result, the importance of diatoms to the phytoplankton community was overemphasized and the contributions of nannoplankton and phytoflagellates were largely underestimated.

Few previous studies have been conducted on phytoplankton in Lake Mohave and Lake Havasu. Priscu (1978) and Priscu et al. (1982) evaluated the effects of fluctuating deep-water discharge on primary productivity and nutrient balance within Lake Mohave. Taylor et al.

(1979) sampled one station during spring, summer, and fall of 1975 in each of Lake Mohave and Lake Havasu.

Methods to Evaluate Phytoplankton Size-Fractioned Biomass

There are, in general, four main methods to evaluate the structure and function of phytoplankton communities in terms of size: (i) Electronic particle counting techniques characterize the entire particle size spectrum based on mean spherical diameter (Sheldon and Parsons 1967, Kitchen et al. 1975). The drawbacks of this technique are that it does not differentiate between detrital material and living cells and it does not produce information on species composition. (ii) Separation of particles with screens or filters to evaluate biomass (McCarthy et al. 1974) and productivity in various size classes (Gelin 1975, Rodhe et al. 1958, Munawar et al. 1978). Screens and filters have variable retention capabilities depending on cell shape and morphology (Sheldon and Sutcliff 1969). Physical damage to cells and, therefore, decreased or altered productivity rates occur even at low filtration pressure (Kalff 1972). As with electronic particle counting techniques, results are difficult to interpret without species composition information. (iii) Microautoradiography provides measurements of photosynthesis of individual species (Knoechel and Kalff 1976, 1978, Paerl and Stull 1979). This technique is extremely time consuming and results are often difficult to interpret (Knoechel and Kalff 1979). (iv) Direct microscopic observations provide information on both species composition and total biomass, provided that a quantitative method such as the inverted microscope technique is utilized (Utermohl

1931,1958). I selected this technique to evaluate the size structure of phytoplankton biomass in lakes Powell, Mead, Mohave, and Havasu.

MATERIALS AND METHODS

Study Site

Lake Powell, the uppermost reservoir on the Colorado River studied, was formed in 1963 with the construction of Glen Canyon Dam. The reservoir, located in northeastern Arizona and southeastern Utah, is 274 km long with a surface area of 653 km^2 and mean depth of 51 m (Table 2). Lake Powell is roughly Y-shaped in plan view with the San Juan River entering 121 km up-lake (Fig. 1). The Colorado and San Juan Rivers provide 96% of the total annual inflow to the reservoir (Iorns et al. 1965).

Lake Mead is located downstream from Lake Powell and the Grand Canyon. The reservoir was formed in 1935 with the construction of Hoover Dam (USDI 1966). Lake Mead extends 183 km from the mouth of the Grand Canyon at Pierce Ferry to Black Canyon. Four large basins comprise the reservoir: Boulder, Virgin, Temple, and Gregg (Fig. 2). Lake Mead has the largest volume of any North American reservoir and is second only to Lake Powell in total surface area (Table 2).

The Colorado River provides 98% of the annual inflow to the reservoir. The remainder of the inflow is from the Virgin and Muddy Rivers which discharge into the Overton Arm and Las Vegas Wash. Las Vegas Wash discharges secondarily-treated sewage and industrial effluent

Table 2. Morphometric characteristics of Lakes Powell, Mead, Mohave, and Havasu.

	Powell	Mead	Mohave	Havasu
Maximim operating level (m)	1128.0	374.0	197.0	137.0
Maximum depth (m)	171.0	180.0	42.0	25.0
Mean depth (m)	51.0	55.0	19.5	9.6
Surface area (km^2)	653.0	660.0	115.0	83.0
Volume ($m^3 X 10^9$)	33.0	36.0	2.3	0.8
Maximum length (km)	269.0	174.0	108.0	65.0
Maximum width (km)	25.0	28.0	6.4	5.0
Shoreline development	26.0	9.7	3.0	-
Discharge depth (m)	70.0	83.0	42.0	15.0
Mean hydraulic retention time (yr)	3.3	3.7	0.2	0.1
Annual discharge ($10^9 m^3$) (mean 1981-1982)	10.0	9.7	9.1	8.2

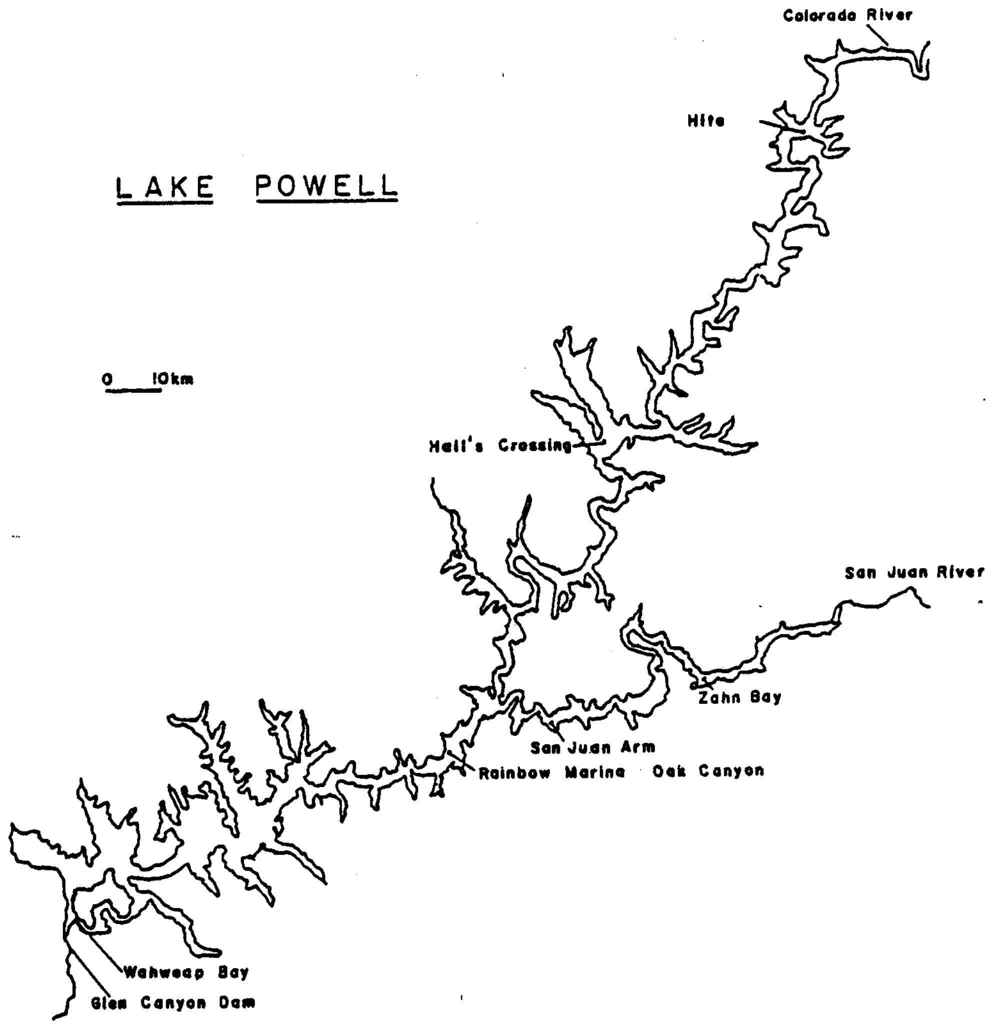

Figure 1. Map of Lake Powell showing sampling stations.

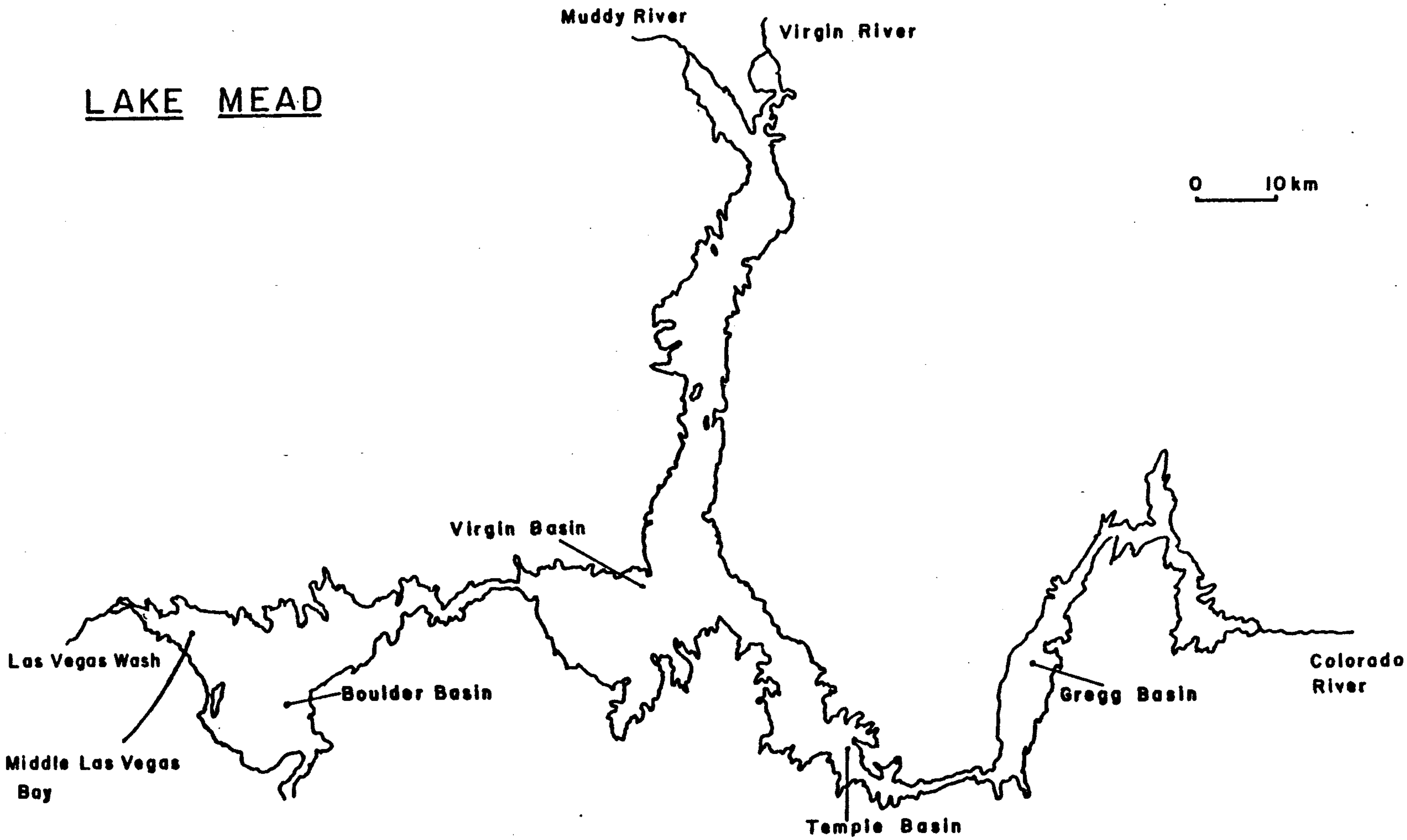

Figure 2. Map of Lake Mead showing the location of the four sampling stations.

from metropolitan Las Vegas into Las Vegas Bay, providing 60% of the inorganic phosphorus loading to Lake Mead in 1981.

Lake Mohave, a warm-monomictic impoundment, is third in the series of reservoirs. The reservoir was formed in 1951 with the construction of Davis Dam. Lake Mohave is only 6.4 km wide and extends 108 km south of Hoover Dam. The reservoir has two small basins at the upper end, Eldorado Canyon and Little Basin, and a third, Cottonwood Basin, located near the middle of the reservoir (Fig. 3). Volume and surface area are small compared to lakes Powell and Mead (Table 2). The only major inflow to the reservoir is the Colorado River via dicharge from Hoover Dam. Hydraulic retention time is 0.24 yr due to rapid flushing from the Colorado River (Paulson et al. 1980). The hypolimnetic discharge at Davis Dam originates at a depth of 42 m.

Formed in 1938 with the construction of Parker Dam, Lake Havasu is the most downstream of the mainstem reservoirs. Lake Havasu morphometry is similar to that of Lake Mohave with a shallow depth, relatively small size, and short retention time (Table 2). The main inflow is supplied by the Colorado River. Lake Havasu has an epilimnetic discharge at Parker Dam in contrast to hypolimnetic discharges in the three upper reservoirs.

A summary of nutrient concentrations including total nitrogen and total phosphorus levels for each reservoir is presented in Table 3. Annual lake mean total-P was extremely low during this study, ranging from 0.009 mg/l in Lake Powell to 0.012 mg/l in lakes Mohave and Havasu.

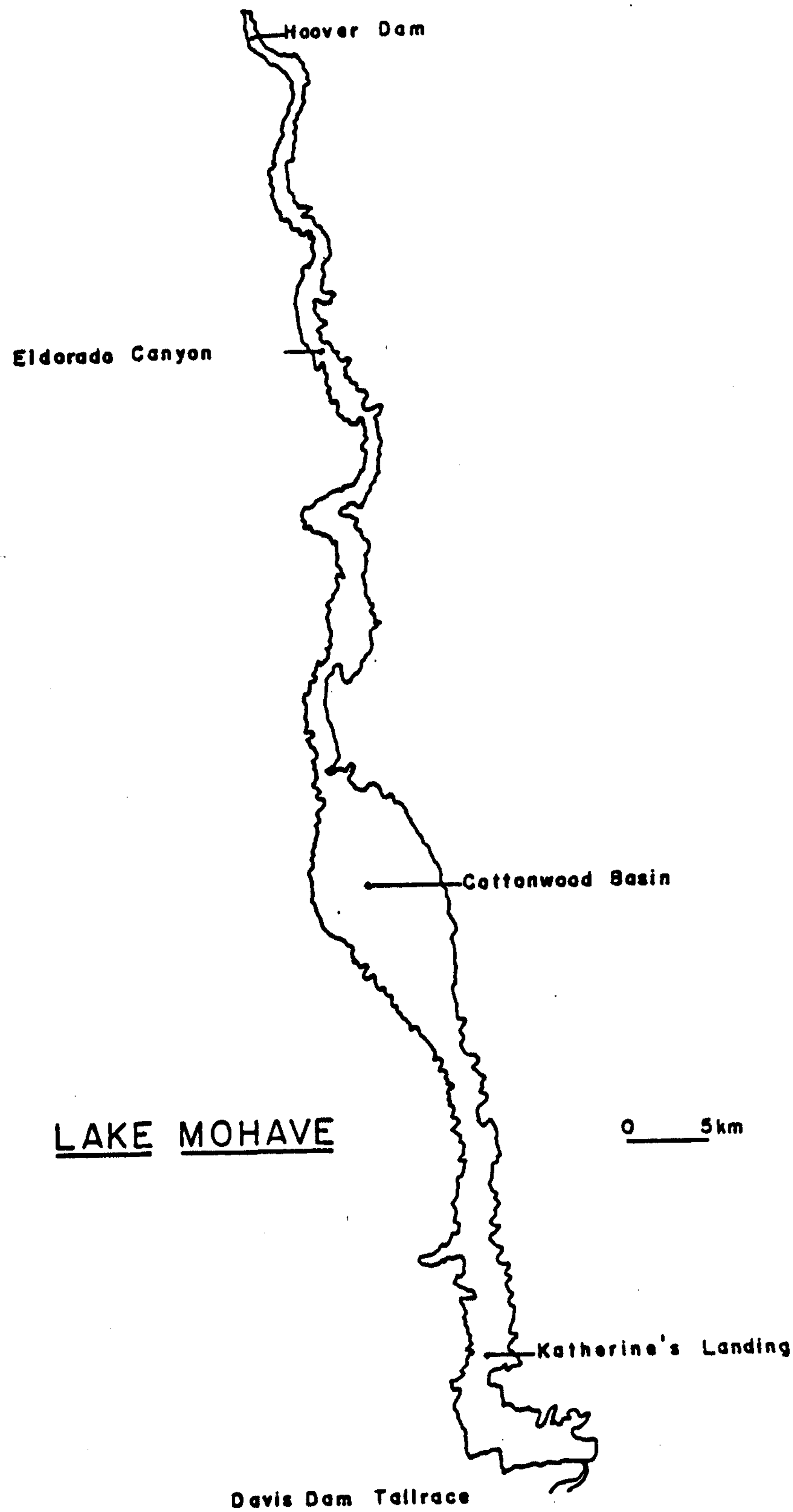

Figure 3. Map of Lake Mohave showing the sampling stations.

Table 3. Mean, maximum, and minimum monthly total nitrogen (mg/l) and total phosphorus concentrations (mg/l) in lakes Powell, Mead, Mohave, and Havasu.

	Powell	Mead	Mohave	Havasu
Mean total-N	0.429	0.364	0.346	0.337
Maximum total-N	0.611	0.766	0.560	0.578
Minimun total-N	0.190	0.120	0.161	0.123
Mean total-P	0.009	0.011	0.012	0.012
Maximum total-P	0.034	0.077	0.032	0.035
Minimum total-P	0.003	0.003	0.005	0.003

Sample Collection

Integrated water samples were collected from surface to 5 m with a 5-cm diameter flexible hose. The hose was lowered to 5 m depth, the top capped and pulled to the surface. The contents were emptied into a 20 l plastic carbuoy. Three tube hauls were taken until approximately 20 l of water was collected. Phytoplankton samples were collected from the well mixed 0-5 m integrated sample and preserved with modified Lugol's solution immediately upon collection (Vollenweider 1969).

Sample Frequency and Station Locations

Figs. 1-4 present maps of each reservoir and the location of sampling stations used during this study. Stations in Lake Powell were selected to coincide with the U. S. Bureau of Reclamation salinity stations. Stations in lakes Mead, Mohave and Havasu were selected to be representative of major lake basins or near important inflows.

In Lake Powell samples were collected monthly from five stations during the period from March 1981 to October 1981 and during January and February 1982. Lake Mead collections were made monthly at four stations from March 1981 to November 1981 and during January and February 1982. Lake Mohave and Lake Havasu collections at three stations in each reservoir were made monthly from April 1981 to November 1981 and during February and March 1982.

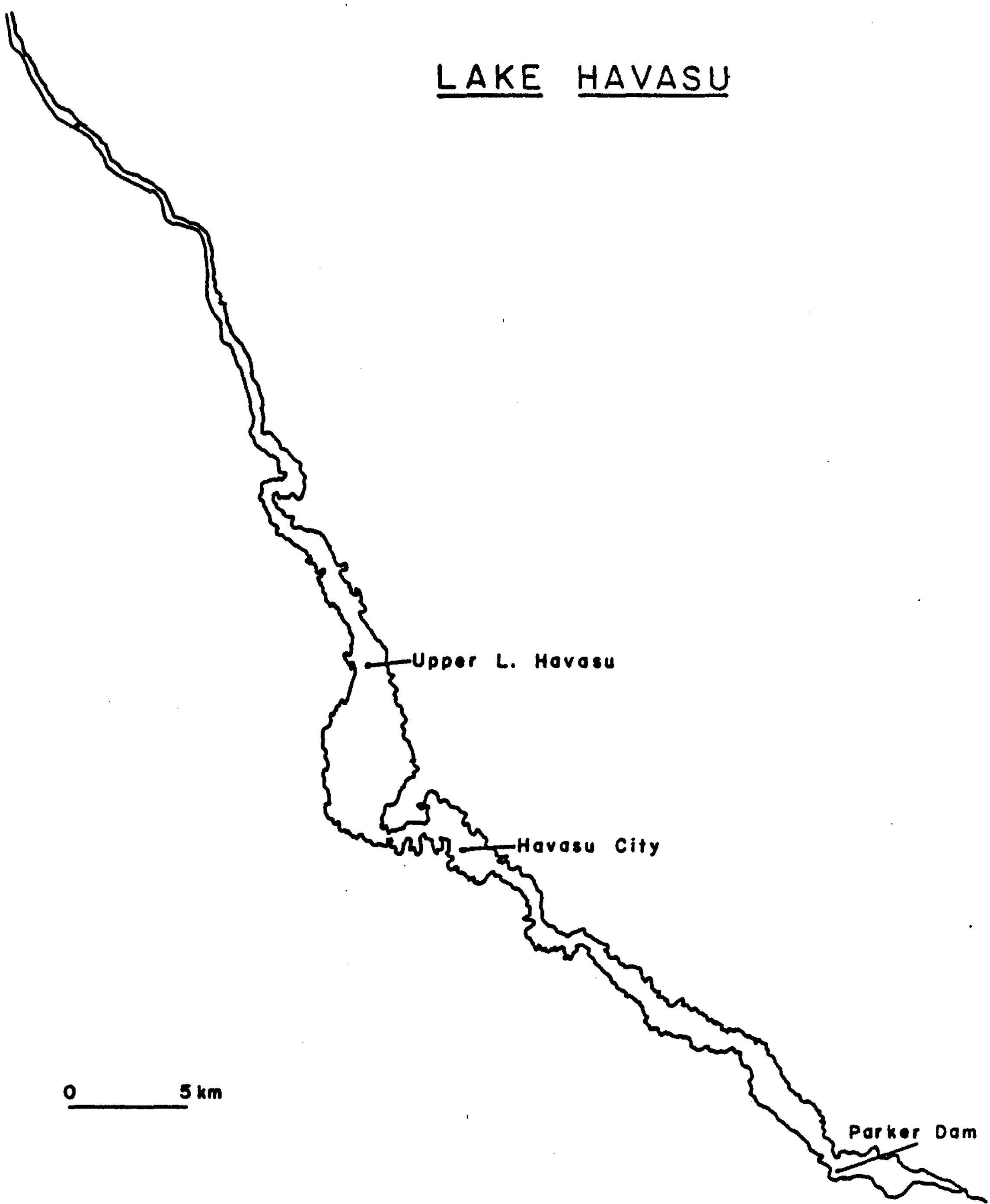

Figure 4. Map of Lake Havasu showing the sampling stations.

Phytoplankton Analysis

Depending on algal density, 10-50 ml of sample was allowed to sediment for a minimum of 24 h in Wild combination chambers and counted with an Olympus IMT phase contrast microscope (Utermohl 1958). Convection currents caused by temperature changes within the chamber impede sedimentation of algal cells, especially the small ultra-plankton (Uehlinger 1964). Therefore, settling chambers and cylinders were covered with an insulated box during sedimentation to reduce the effects of air currents and maintain the chambers at relatively constant room temperature of 20 °C.

When air currents and abrupt temperature changes were eliminated, 24 h proved adequate to sediment phytoplankton in 12 cm high and 50 ml volume cylinders. Furet and Benson-Evans (1982) recommended 3 hours settling time per cm height of the sedimentation chamber. I followed the recommendations of Lund et al. (1958) of 12 cm per day and Willen (1976) who reported that 24 h was sufficient to settle plankton in 50 ml chambers.

I examined the samples at several microscopic magnifications, depending on the algal size fraction. The procedure was as follows:

1. Cells with the longest linear dimension greater than 64 um were counted at 100X magnification.
    a. Common species were counted and identified in two-0.4 mm wide transects across the 25 mm diameter plate chamber. I examined 4% of the sample at this magnification.
    b. Less common and rare species were counted by scanning the

entire 510 mm^2 area plate chamber.

2. Cells with longest dimension greater than 20 um and less than 64 um were counted at 200X magnification.

    a. Common species were counted in two-0.2 mm wide transects with 2% of the sample being examined.

    b. The entire chamber (100% of the sample) was scanned for rare species.

3. Cells less than 20 um were counted at 400X magnification in two-0.1 mm wide cross diameter transects (1% of the sample examined).
4. Cells generally less than 3 um which could not be counted or identified at 400X were counted in 10 mm long by 0.04 mm wide transects under oil immersion (1000X).

At least 300 units were counted for each sample. A unit is defined as a filament, colony, or solitary cell. Counting error of +12% was achieved with this count size, assuming random distribution (Lund et al. 1958).

Diatoms were identified from permanent slides prepared by heating concentrated samples to 550 °C for 30 minutes and then mounted in Hyrax medium (Patrick and Reimer 1966).

Cell volumes were calculated based on measurements of at least 30 individuals of each species and geometrical formulae which most closely approximate cell shape (Rodhe et al. 1958, Findenegg 1969). Cell volume

was converted to biomass assuming a specific gravity of 1 (Willen 1959, Nauwerck 1963, Oliver et al. 1981).

Algal size fractions were based on the longest linear cell dimension, measured with an ocular micrometer. The phytoplankton assemblage was divided into the following six size classes or fractions based on Munawar and Munawar's (1978) scheme, with slight modification. Netplankton are defined as algae larger than 64 um and nannoplankton less than 64 um. The rationale for this arbitrary scheme was that early plankton studies in North America used nets with 64 um mesh (Munawar et al. 1978). The 64 um size separation is also close to the midpoint of the the size range used to describe nannoplankton and netplankton by various investigators (Table 1).

<5 um	Size Class 1--Nannoplankton
>5<11 um	Size Class 2
>11<21 um	Size Class 3
>21<44 um	Size Class 4
>44<64 um	Size Class 5
>64 um	Size Class 6--Netplankton

The most commonly used taxonomic references were: Bourelly (1966, 1968, 1970), Czarnecki and Blinn (1977, 1978), Desikachary (1959), Geitler (1932), Huber-Pestalozzi (1938-1968), Patrick and Reimer (1966, 1975), Prescott (1951), Skuja (1948, 1956, 1964), and Starmach (1968, 1974).

Nutrients

Ammonia was analyzed according to Liddicoat et al. (1975); nitrate followed the method of Kamphake et al. (1967); total nitrogen was analyzed according to D'Elia et al. (1977) and APHA (1975). Dissolved phosphorus analysis followed the procedures of Strickland and Parsons (1972) and APHA (1975); orthophosphate procedures followed Strickland and Parsons (1972) and Goldman (1974), and total phosphorus was analyzed according to the methods of Strickland and Parsons (1972) and APHA (1975). Photometric determinations were made with a Perkin Elmer Model 55 Spectophotometer. Further details on chemical methods are found in Kellar et al. (1980).

RESULTS

Inflows and Reservoir Surface Water Temperatures

During the period (May-July) of high flow into Lake Powell (Table 4), the inflow water was relatively warm at 15-28 °C (Table 5). Peak inflow occurred in June as a result of snowmelt. Inflow volumes were low throughout the summer months and increased in September and October (Table 4). Inflow water temperatures were generally warmer than Lake Powell surface temperatures during early spring (Tables 5, 6). During May and June, surface water temperatures were higher than inflows due to surface heating by solar insolation. Inflow temperatures in June were 20.2 °C compared to lake temperatures of 21-23.5 °C. Lake Powell surface temperatures reach an annual maximum of 25-27 °C in July and August. After reaching winter minima, surface temperatures begin to increase again in April and May (Table 6).

The Colorado River provides 98% of the inflow into Lake Mead. Las Vegas Wash which enters Lake Mead at Las Vegas Bay provides only 1% of the inflow volume into Lake Mead but is an important source of nutrients. Lake Mead surface temperatures followed a pattern similar to Lake Powell with maxima reached during July and August; however, monthly surface temperatures are generally 1-4 °C higher in Lake Mead than in Lake Powell. Peak inflows occurred during the months of July, August,

Table 4. Monthly reservoir flow volume ($m^3 \times 10^8$).

Month	*Combined Powell inflows	Glen Canyon Dam	Hoover Dam	Davis Dam	Parker Dam
Mar 1981	4.62	5.22	10.05	10.65	8.74
Apr	4.62	5.51	12.53	12.77	10.50
May	7.44	6.53	10.57	10.06	8.37
Jun	11.42	6.32	10.30	12.06	10.17
Jul	5.27	10.32	10.65	13.28	11.44
Aug	3.24	10.93	11.29	12.45	10.76
Sep	5.50	8.10	8.17	7.78	7.03
Oct	7.53	7.56	4.68	4.78	4.13
Nov	4.98	7.71	4.79	3.86	3.12
Dec	4.81	10.31	4.90	4.15	3.68
Jan 1982	4.80	11.05	5.71	4.74	4.20
Feb	6.66	8.32	6.77	6.85	6.01
Mar	8.25	6.23	9.77	9.18	8.02
Total	79.14	104.11	110.18	112.61	96.17

* Colorado River
San Juan River
Green River

Table 5. Inflow and outflow surface temperatures (°C).

	Cataract Canyon	Glen Canyon	Grand Canyon	Hoover Dam	Davis Dam	Parker Dam
Mar 1981	10.0	9.4	12.7	-	13.3	13.4
Apr	16.9	9.3	16.8	12.8	13.6	17.0
May	15.4	12.8	17.7	13.0	16.0	21.9
Jun	20.2	8.7	21.0	12.5	17.1	22.5
Jul	27.9	11.7	-	12.7	17.7	26.5
Aug	25.1	-	16.8	-	19.0	29.7
Sep	21.3	-	15.5	-	-	32.4
Oct	-	10.5	12.3	-	16.2	25.0
Nov	-	-	-	12.5	16.5	19.0
Dec	-	-	-	-	-	-
Jan 1982	-	-	8.5	-	-	-
Feb	5.4	8.0	-	12.0	12.0	9.4
Mar	9.0	8.0	10.5	11.7	11.7	14.5

Table 6. Monthly surface temperatures (°C) by station at four reservoirs.

	1981										1982		
	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
LAKE POWELL													
Hite	10.4	14.9	16.0	22.5	26.5	26.0	24.8	19.5	-	-	8.5	7.9	9.0
Zahn Bay	-	16.5	17.1	23.5	26.0	26.1	24.4	19.0	-	-	8.5	9.1	-
Hall's Crossing	10.8	15.8	15.9	21.0	26.8	25.5	25.3	19.4	-	-	8.6	8.5	8.4
Oak Canyon	10.4	14.1	15.9	21.3	25.5	25.0	24.2	19.0	-	-	8.7	8.6	9.2
Wahweap Bay	11.0	15.2	15.5	22.1	25.7	24.8	24.5	18.5	-	-	8.4	9.1	8.4
LAKE MEAD													
Gregg Basin	14.6	16.7	20.9	26.3	29.8	28.5	26.3	20.6	17.8	-	12.5	12.5	13.5
Virgin Basin	13.9	16.5	19.9	25.4	28.1	28.1	26.6	20.6	17.7	-	12.0	12.5	12.0
Boulder Basin	13.9	16.8	19.6	24.8	27.0	28.0	26.4	20.6	17.5	-	12.0	12.0	14.0
Middle Las Vegas Bay	14.2	17.5	21.9	24.8	28.6	28.3	26.5	20.6	17.1	-	12.0	12.0	13.7
LAKE MOHAVE													
Eldorado Canyon	13.7	13.0	14.7	20.4	24.0	24.9	19.0	23.4	14.0	-	-	9.8	13.0
Cottonwood Basin	12.5	15.0	20.3	21.4	25.7	27.9	30.2	24.3	16.5	-	-	9.6	13.0
Katherine's Landing	12.4	14.9	18.3	20.5	23.2	24.9	29.2	22.3	16.0	-	-	9.4	13.7
LAKE HAVASU													
Upper Lake Havasu	13.0	16.0	20.0	23.3	25.7	28.5	26.4	-	16.0	-	-	8.7	12.0
Havasu City-South	13.4	17.0	21.6	23.4	26.3	28.3	29.8	-	17.5	-	-	9.0	13.5
Parker Dam	13.3	16.6	21.7	22.1	25.5	27.8	30.7	23.6	18.5	-	-	9.3	10.8

December and January (Table 4). Inflow temperatures into Lake Mead measured in the Grand Canyon are lower than the surface waters during all months except in March and April (Table 5).

The only major inflow into Lake Mohave is from hypolimnetic releases from Hoover Dam which were high during March through August (Table 4). Inflow temperatures to Lake Mohave from Hoover Dam were nearly constant throughout the year, averaging 11-13 °C. Surface temperatures were lower in Lake Mohave than in Lake Mead during most of the year. Temperature differences between stations were greatest in Lake Mohave, with Eldorado Canyon surface temperatures generally lower than the two down-lake stations (Table 6). Surface water temperatures in May ranged from 14.7 °C at Eldorado Canyon to 20.3 °C at Cottonwood Basin.

Lake Havasu receives its main inflow from Davis Dam. Total inflow and seasonal inflow patterns were similar to those at Hoover Dam, which are highest during spring and summer (Table 4). Discharge temperatures from Davis Dam ranged from 12-13 °C in February through March to 19 °C in August. Inflow temperatures were lower than lake surface temperatures during most of the year. Monthly temperature differences between Lake Havasu stations were small except during September when Upper Lake Havasu was 3-4 °C lower than the down-lake stations.

Nutrients

Total nitrogen

Total nitrogen concentrations in Lake Powell were highest at Wahweap Bay where values averaged 0.540 mg/l during the study. Total-N concentrations at Hite, the most up-lake station, averaged 0.514 mg/l. Total-N concentrations decreased down-lake from Hall's Crossing to Oak Canyon and increased at Wahweap Bay (Table 7). Seasonally, the highest total-N concentrations occurred during April and May when total-N at Wahweap Bay was 1.32 and 1.61 mg/l, respectively. Lowest seasonal concentrations occurred during the summer months of June-September.

Total nitrogen concentrations in Lake Mead were highest at Middle Las Vegas Bay where values averaged 0.416 mg/l. Total-N was lowest in Gregg Basin and increased down-lake at Virgin and Boulder Basins. Seasonal total-N concentrations were highest during the winter when concentrations were 0.504 and 0.507 mg/l in February and March, respectively. Total-N concentrations were lowest during late summer and early fall. Annual total-N of 0.364 mg/l in Lake Mead was lower than the 0.429 mg/l concentration in Lake Powell.

Total- N concentrations in Lake Mohave were highest at Eldorado Canyon where values averaged 0.389 mg/l. Total-N concentrations decreased down-lake at Cottonwood Basin and increased at Katherine's Landing. Seasonal values were highest during March-May and lowest in the summer months of July-September. Total-N concentrations in Lake

Table 7. Monthly surface total nitrogen (mg/l) by station.

	1981										1982			Mean
	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	
LAKE POWELL														
Hite	0.488	0.479	0.696	0.622	0.227	0.441	0.461	0.580	-	-	0.571	0.547	0.541	0.514
Zahn Bay	-	0.510	0.244	0.250	0.257	0.260	0.282	0.407	-	-	0.451	0.441	0.511	0.361
Hall's Crossing	0.491	0.425	0.350	0.399	0.313	0.315	0.316	0.375	-	-	0.457	0.508	0.668	0.420
Oak Canyon	0.405	0.479	0.327	0.391	0.239	0.281	0.233	0.288	-	-	0.420	0.468	0.551	0.371
Wahweap Bay	0.412	1.316	1.611	0.330	0.278	0.296	0.190	0.225	-	-	0.307	0.458	0.521	0.540
Mean	0.449	0.641	0.646	0.398	0.263	0.319	0.296	0.375	-	-	0.441	0.484	0.558	
LAKE MEAD														
Gregg Basin	0.381	0.361	0.366	0.330	0.153	0.192	0.220	0.255	0.324	-	0.323	0.408	0.582	0.325
Virgin Basin	0.422	0.340	0.340	0.614	0.230	0.204	0.260	0.295	0.520	-	0.245	0.398	0.476	0.362
Boulder Basin	0.458	0.494	0.629	0.210	0.221	0.204	0.153	0.236	0.318	-	0.405	0.691	0.434	0.371
Middle Las Vegas Bay	0.454	0.388	0.488	0.183	0.379	0.766	0.370	0.270	0.301	0.398	0.351	0.518	0.536	0.416
Mean	0.429	0.396	0.456	0.334	0.246	0.342	0.251	0.264	0.366	0.398	0.331	0.504	0.507	
LAKE MOHAVE														
Eldorado Canyon	0.433	0.509	0.494	0.322	0.221	0.290	0.277	0.290	0.560	-	0.366	0.497	0.409	0.389
Cottonwood Basin	0.457	0.340	0.385	0.229	0.165	0.161	0.246	0.290	0.279	-	0.373	0.452	0.409	0.316
Katherine's Landing	0.475	0.365	0.403	0.432	0.501	0.272	0.296	0.338	0.310	-	0.345	0.372	0.470	0.382
Mean	0.455	0.405	0.427	0.328	0.296	0.241	0.273	0.306	0.383	-	0.361	0.440	0.429	
LAKE HAVASU														
Upper Lake Havasu	0.447	0.433	0.305	0.287	0.257	0.260	0.333	0.386	0.384	-	0.448	0.446	0.444	0.369
Havasu City-South	0.405	0.454	0.202	0.287	0.260	0.229	0.578	0.405	0.322	-	0.335	0.381	0.370	0.352
Parker Dam	0.398	0.440	0.209	0.368	0.123	0.260	0.364	0.362	0.314	-	0.342	0.318	0.364	0.322
Mean	0.416	0.442	0.239	0.314	0.213	0.250	0.425	0.384	0.340	-	0.375	0.382	0.393	

Havasu were simlar to those of Lake Mohave. Total-N concentrations were highest at the most up-lake station, Upper Lake Havasu, and decreased down-lake. Seasonal total- N concentrations in Lake Havasu were lowest during the summer months of July and August.

Inorganic nitrogen (ammonia + nitrate)

Inorganic nitrogen concentrations were highest at Hite where values averaged 0.274 mg/l during the study (Table 8). Inorganic-N concentrations decreased down-lake from Hall's Crossing to Wahweap Bay. Seasonal inorganic-N concentrations of 0.332 mg/l were highest in January. Lowest values of 0.075 and 0.090 mg/l occurred in July and September, respectively.

Inorganic nitrogen concentrations in Lake Mead were highest at the most up-lake stations in Gregg and Virgin Basins. Values decreased in Boulder Basin and increased in Middle Las Vegas Bay. Seasonal inorganic-N concentrations were highest in Lake Mead during spring and winter, minimum values of 0.041 mg/l were observed in September.

Monthly patterns of inorganic-N concentrations in lakes Mead, Mohave and Havasu were similar with highest concentrations occurring during late winter and spring, followed by decreasing concentrations during the period of increasing phytoplankton biomass. Inorganic-N concentrations in all reservoirs were low during July through October. Annual means were highest in Eldorado Canyon in Lake Mohave, and in Upper Lake Havasu.

Table 8. Monthly surface inorganic (nitrate + ammonia) nitrogen (mg/l).

	1981										1982			Mean
	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	
LAKE POWELL														
Hite	0.270	0.249	0.374	0.210	0.056	0.248	0.192	0.278	-	-	0.498	0.293	0.345	0.274
Zahn Bay	-	0.111	0.137	0.066	0.011	0.072	0.057	0.156	-	-	0.396	0.255	0.251	0.151
Hall's Crossing	0.276	0.234	0.211	0.189	0.148	0.170	0.134	0.202	-	-	0.328	0.318	0.303	0.228
Oak Canyon	0.288	0.273	0.193	0.139	0.097	0.122	0.039	0.094	-	-	0.240	0.278	0.279	0.186
Wahweap Bay	0.229	0.238	0.161	0.069	0.064	0.004	0.028	0.059	-	-	0.200	0.176	0.242	0.134
Mean	0.266	0.221	0.215	0.135	0.075	0.123	0.090	0.158	-	-	0.332	0.264	0.284	
LAKE MEAD														
Gregg Basin	0.277	0.272	0.161	0.175	0.144	0.125	0.090	0.121	0.210	-	0.164	0.269	0.276	0.190
Virgin Basin	0.269	0.279	0.213	0.136	0.118	0.087	0.069	0.140	0.201	-	0.255	0.280	0.276	0.194
Boulder Basin	0.247	0.266	0.160	0.009	0.002	0.004	0.002	0.013	0.182	-	0.218	0.247	0.257	0.134
Middle Las Vegas Bay	0.237	0.234	0.260	0.015	0.055	0.219	0.003	0.063	0.165	-	0.263	0.253	0.247	0.168
Mean	0.258	0.263	0.199	0.084	0.080	0.109	0.041	0.084	0.190	-	0.225	0.262	0.264	
LAKE MOHAVE														
Eldorado Canyon	0.270	0.280	0.335	0.085	0.040	0.030	0.096	0.006	0.233	-	-	0.164	0.272	0.165
Cottonwood Basin	0.223	0.234	0.184	0.156	0.006	0.012	0.015	0.005	0.068	-	-	0.256	0.220	0.125
Katherine's Landing	0.241	0.170	0.212	0.167	0.044	0.034	0.029	0.008	0.139	-	-	0.178	0.156	0.125
Mean	0.245	0.228	0.244	0.136	0.030	0.025	0.047	0.006	0.147	-	-	0.199	0.216	
LAKE HAVASU														
Upper Lake Havasu	0.180	0.137	0.191	0.154	0.114	0.028	0.055	0.012	0.101	-	-	0.177	0.193	0.122
Havasu City-South	0.181	0.179	0.189	0.143	0.053	0.080	0.034	0.004	0.069	-	-	0.131	0.189	0.114
Parker Dam	0.181	0.149	0.153	0.124	0.062	0.017	0.018	0.027	0.052	-	-	0.127	0.157	0.097
Mean	0.181	0.155	0.178	0.140	0.076	0.042	0.036	0.014	0.074	-	-	0.145	0.180	

Total phosphorus

Total-P concentrations were generally low throughout the the four reservoirs. Highest values were measured at the inflow stations in Hite and Zahn Bay, and at Middle Las Vegas Bay, near the inflow of Las Vegas Wash (Table 9). Total-P in Lake Powell was highest during the peak inflow month of June (Tables 4, 9). Total-P concentrations decreased down-lake from 0.015 mg/l at Hite to 0.005 mg/l at Wahweap Bay. Seasonally, total-P concentrations of 0.005 in January were the lowest measured during the study in Lake Powell.

Total-P concentrations in Lake Mead were highest at Middle Las Vegas Bay where values averaged 0.024 mg/l. Total-P concentrations were less than 0.010 mg/l at Gregg, Virgin, and Boulder Basins (Table 9). Seasonally, the highest total-P concentrations occurred in August.

Total phosphorus concentrations in Lake Mohave were highest at Eldorado Canyon where values averaged 0.015 mg/l. Total-P concentrations decreased down-lake to 0.011 mg/l at each of Cottonwood Basin and Katherine's Landing. Seasonally, the highest total-P concentrations occurred in June.

Total-P values in Lake Havasu were highest at the inflow station, Upper Lake Havasu, where values averaged 0.014 mg/l during the study. Lowest total-P concentrations were measured at Havasu City. Seasonally, the highest total-P concentrations occurred in March, and the lowest during April-June.

Table 9. Monthly surface total phosphorus (mg/l) by station.

	1981										1982			Mean
	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	
LAKE POWELL														
Hite	0.009	0.011	0.021	0.034	0.015	0.020	0.021	0.012	-	-	0.006	0.010	0.008	0.015
Zahn Bay	-	0.019	0.018	0.026	0.016	0.009	0.008	0.011	-	-	0.005	0.007	0.012	0.013
Hall's Crossing	0.007	0.011	0.014	0.016	0.011	0.004	0.006	0.004	-	-	0.006	0.010	0.008	0.009
Oak Canyon	0.009	0.006	0.004	0.006	0.018	0.013	0.006	0.004	-	-	0.004	0.008	0.006	0.008
Wahweap Bay	0.004	0.008	0.003	0.006	0.008	0.003	0.003	0.005	-	-	0.003	0.005	0.005	0.005
Mean	0.007	0.011	0.012	0.018	0.014	0.010	0.009	0.007			0.005	0.008	0.008	
LAKE MEAD														
Gregg Basin	0.008	0.004	0.004	0.006	0.008	0.015	0.010	0.008	0.004	-	0.006	0.005	0.008	0.007
Virgin Basin	0.004	0.004	0.004	0.005	0.007	0.003	0.004	0.005	0.004	-	0.008	0.004	0.004	0.005
Boulder Basin	0.013	0.009	0.010	0.006	0.005	0.005	0.004	0.016	0.005	-	0.008	0.009	0.023	0.009
Middle Las Vegas Bay	0.012	0.011	0.035	0.015	0.019	0.077	0.021	0.011	0.062	-	0.006	0.008	0.010	0.024
Mean	0.009	0.007	0.013	0.008	0.010	0.025	0.010	0.010	0.019		0.007	0.007	0.011	
LAKE MOHAVE														
Eldorado Canyon	0.021	0.012	0.014	0.032	0.014	0.019	0.015	0.017	0.013	-	0.009	0.008	0.008	0.015
Cottonwood Basin	0.019	0.008	0.010	0.009	0.011	0.007	0.009	0.012	0.011	-	0.014	0.011	0.010	0.011
Katherine's Landing	0.024	0.006	0.005	0.011	0.009	0.012	0.011	0.011	0.010	-	0.011	0.011	0.008	0.011
Mean	0.021	0.009	0.010	0.017	0.011	0.013	0.012	0.013	0.011	-	0.011	0.010	0.009	
LAKE HAVASU														
Upper Lake Havasu	0.028	0.010	0.007	0.010	0.014	0.012	0.014	0.015	0.013	-	0.015	0.017	0.017	0.014
Havasu City-South	0.019	0.008	0.005	0.006	0.010	0.007	0.012	0.010	0.013	-	0.010	0.012	0.012	0.010
Parker Dam	0.018	0.007	0.003	0.010	0.009	0.009	0.014	0.016	0.018	-	0.014	0.026	0.008	0.013
Mean	0.022	0.008	0.005	0.009	0.011	0.009	0.013	0.014	0.015	-	0.013	0.018	0.012	

Ortho-phosphorus

Ortho-P concentrations in lakes Powell, Mead, Mohave, and Havasu were low throughout the year (Table 10). Ortho-P concentrations were highest in Lake Powell at Hite where values averaged 0.003 mg/l during the study. Concentrations were similar at the down-lake stations where values of 0.002 mg/l were measured at each station. Seasonally, ortho-P was highest in June during the peak river inflows.

Ortho-P concentrations were highest in Lake Mead at Middle Las Vegas Bay. Values averaged 0.004 mg/l during the study. Concentrations were similar at the other three Lake Mead stations. Seasonally, ortho-P concentrations were highest during December, and lowest values of 0.001 mg/l occurred in May.

Ortho-P was highest in Lake Mohave at Eldorado Canyon where values averaged 0.004 mg/l. Concentrations were low at the down-lake stations. Lake Havasu ortho-P concentrations were similar at all stations throughout the year, except for a somewhat higher September value of 0.007 mg/l at Havasu City.

Phytoplankton Biomass, Species Composition and Succession

Lake Powell

Phytoplankton biomass in Lake Powell was highest at Zahn Bay where values averaged 1.97 g/m^3 during the study (Table 11). The San Juan Arm station at Zahn Bay and upper Lake Powell at Hite contributed the

Table 10. Monthly surface ortho-phosphorus (mg/l) by station.

	1981										1982			Mean
	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	
LAKE POWELL														
Hite	0.002	0.001	0.001	0.005	0.003	0.002	0.001	0.004	-	-	0.003	0.002	0.002	0.003
Zahn Bay	-	0.002	0.001	0.002	0.002	0.001	0.002	0.001	-	-	0.002	0.002	0.001	0.002
Hall's Crossing	0.002	0.001	0.001	0.006	0.003	0.001	0.001	0.003	-	-	0.002	0.002	0.001	0.002
Oak Canyon	0.001	0.004	0.001	0.002	0.002	0.001	0.001	0.001	-	-	0.003	0.004	0.003	0.002
Wahweap Bay	0.002	0.005	0.001	0.003	0.002	0.001	0.001	0.001	-	-	0.003	0.003	0.002	0.002
Mean	0.002	0.003	0.001	0.004	0.002	0.001	0.001	0.002	-	-	0.003	0.003	0.002	
LAKE MEAD														
Gregg Basin	0.002	0.001	0.001	0.002	0.001	0.001	0.002	0.001	0.002	-	0.002	0.002	0.003	0.002
Virgin Basin	0.002	0.003	0.001	0.002	0.002	0.002	0.002	0.002	0.002	-	0.004	0.001	0.002	0.002
Boulder Basin	0.003	0.001	0.001	0.001	0.005	0.002	0.002	0.002	0.003	-	0.007	0.003	0.003	0.003
Middle Las Vegas Bay	0.003	0.005	0.001	0.002	0.003	0.007	0.004	0.004	0.006	0.005	0.003	0.005	0.002	0.004
Mean	0.003	0.003	0.001	0.002	0.003	0.003	0.003	0.002	0.003	0.005	0.004	0.003	0.003	
LAKE MOHAVE														
Eldorado Canyon	0.006	0.010	0.006	0.001	0.001	0.002	0.002	0.001	0.004	-	0.003	0.005	0.004	0.004
Cottonwood Basin	0.003	0.002	0.002	0.001	0.001	0.001	0.002	0.002	0.002	-	0.002	0.002	0.002	0.002
Katherine's Landing	0.001	0.002	0.003	0.003	0.001	0.002	0.002	0.001	0.002	-	0.002	0.002	0.002	0.002
Mean	0.003	0.005	0.004	0.002	0.001	0.002	0.002	0.001	0.003	-	0.002	0.003	0.003	
LAKE HAVASU														
Upper Lake Havsau	0.001	0.002	0.002	0.003	0.001	0.002	0.002	0.002	0.002	-	0.001	0.003	0.002	0.002
Havasu City-South	0.001	0.001	0.002	0.002	0.001	0.002	0.007	0.003	0.004	-	0.001	0.002	0.002	0.002
Parker Dam	0.002	0.003	0.001	0.003	0.001	0.003	0.003	0.004	0.004	-	0.002	0.002	0.002	0.003
Mean	0.001	0.002	0.002	0.003	0.001	0.002	0.004	0.003	0.003	-	0.001	0.002	0.002	

Table 11. Seasonal mean phytoplankton biomass and percentage biomass by size in Lake Powell stations from March 1981 to February 1982.

	Phytoplankton biomass (g/m3)	Percentage biomass by size (um)					
		<5	>5<11	>11<21	>21<44	>44<64	>64
Hite							
Spring	0.710	1.0	5.5	7.1	20.7	5.8	59.9
Summer	1.510	6.7	11.2	18.0	39.3	12.6	12.2
Fall	0.478	1.8	18.7	37.8	9.9	21.4	10.5
Winter	0.500	1.6	6.8	11.1	27.7	0.9	52.0
Mean	0.964	4.7	9.9	15.8	32.5	10.3	26.8
Hall's Crossing							
Spring	0.354	4.0	9.0	2.5	33.7	18.6	32.1
Summer	0.792	8.1	10.7	6.1	41.8	12.2	21.1
Fall	0.835	7.4	16.4	2.3	39.1	7.8	27.1
Winter	0.409	2.5	5.6	2.3	34.5	1.7	53.3
Mean	0.614	6.7	10.6	4.5	39.3	10.8	28.2
Zahn Bay							
Spring	2.510	2.1	2.9	0.8	7.3	6.6	70.3
Summer	1.225	12.3	9.1	11.6	57.1	4.1	5.6
Fall	5.596	1.0	3.5	3.7	0.9	7.4	83.6
Winter	0.374	7.6	10.1	2.7	40.7	2.0	36.9
Mean	1.974	3.8	4.6	4.0	19.0	6.2	62.4
Oak Canyon							
Spring	0.341	3.9	10.2	2.0	54.8	14.9	14.2
Summer	0.438	4.7	13.1	6.9	39.5	22.4	13.5
Fall	0.777	3.1	26.6	12.6	46.0	1.2	10.6
Winter	0.499	2.1	8.2	1.1	44.7	0.7	43.6
Mean	0.455	3.7	13.7	5.5	45.2	12.3	19.7
Wahweap Bay							
Spring	0.628	1.8	6.0	1.7	40.2	9.5	40.8
Summer	0.430	5.8	11.5	7.3	45.3	13.3	16.7
Fall	2.204	2.0	12.9	4.4	11.1	2.2	67.3
Winter	0.237	6.9	13.5	2.3	57.5	3.3	16.3
Mean	0.628	3.3	10.5	4.2	32.7	7.5	41.7

greatest biomass in Lake Powell. Phytoplankton biomass was high at Hite, located closest to the Colorado River inflow, during April, and July through September. Zahn Bay contributed greatly to Lake Powell phytoplankton biomass in April and July, with values of 4.2 and 5.6 g/m^3, respectively. The order of decreasing annual biomass concentrations were Hite (1.0 g/m^3), Wahweap Bay and Hall Crossing (0.6 g/m^3), and Oak Canyon (0.5 g/m^3).

Seasonally, three small biomass peaks were evident; occurring in April, July, and October (Fig. 5). Biomass was lowest in Lake Powell in May-June and during late winter-early spring. Annual reservoir phytoplankton biomass was 0.96 g/m^3 and biomass weighted by station, which reduced the contribution of Zahn Bay, was 0.78 g/m^3.

Lake Powell was dominated by diatoms, dinoflagellates, and cryptomonads with annual mean biomass contributions of 30, 29, and 22 percent, respectively. Phytoflagellates (dinoflagellates, cryptomonads, and chrysomonads) as a group were most abundant contributing 60 percent of total lake-wide biomass. The quantitative importance of greens and blue-greens to total biomass was low, each contributing less than 7 percent of total biomass.

Seasonal fluctuations in taxonomic group biomass are presented in Fig. 6. Group biomass succession shows dinoflagellates contributing 50% of total biomass in March followed by a short diatom peak in April. Dinoflagellates dominated the biomass throughout the summer months. Diatoms were again the main component in October, contributing nearly 75% of total biomass. Cryptomonads were dominant in winter, followed in February by nearly equal biomass contributions of diatoms

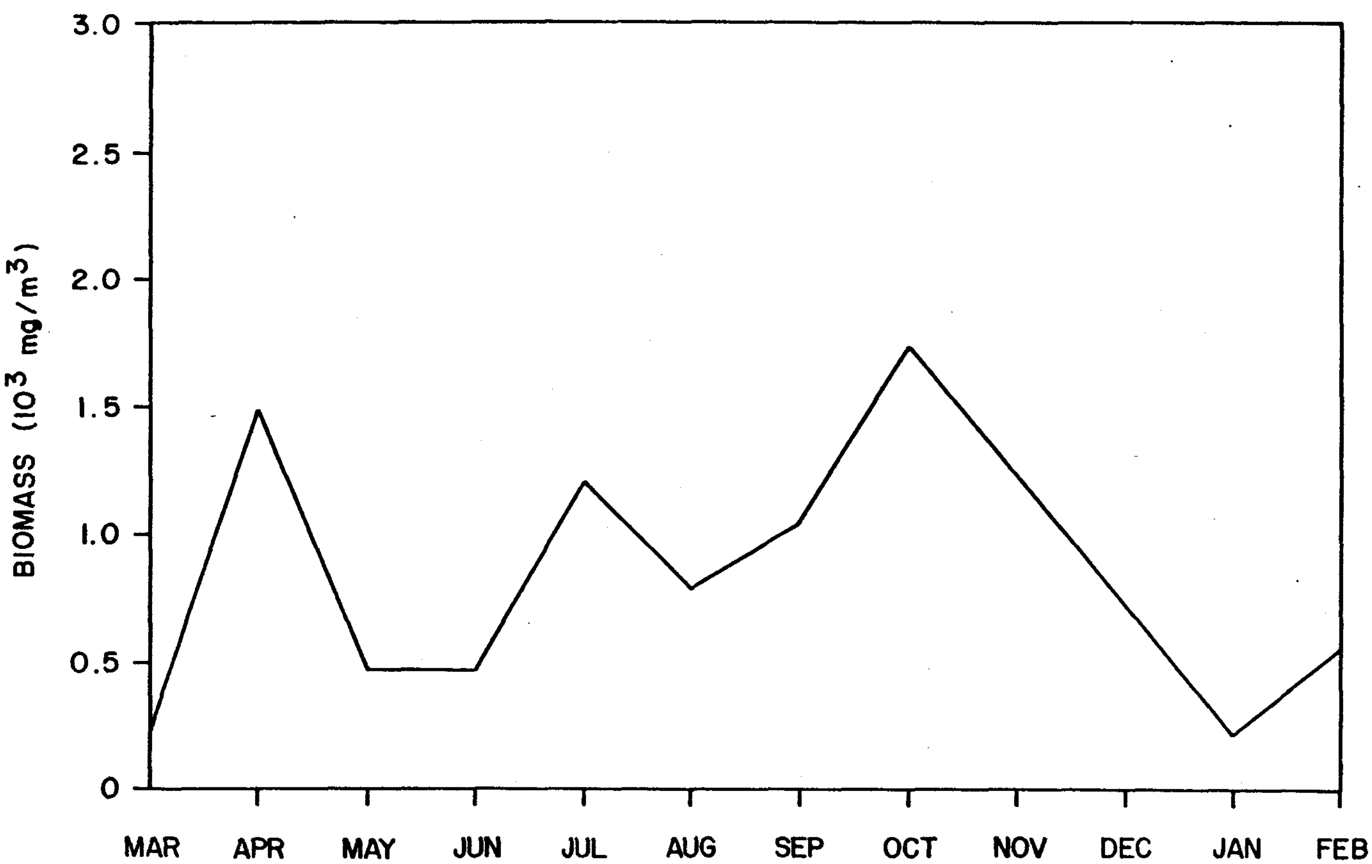

Figure 5. Monthly phytoplankton biomass in Lake Powell.

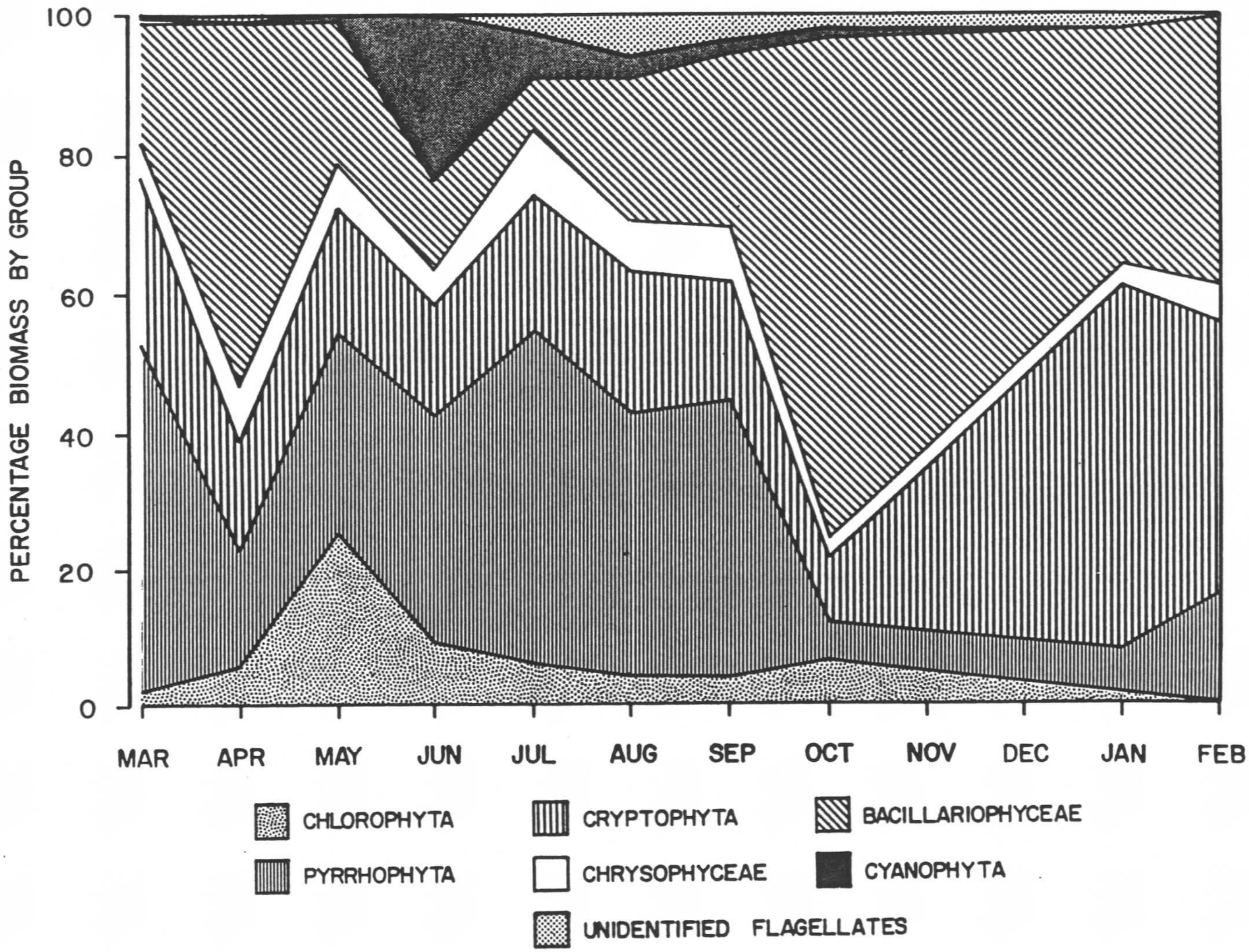

Figure 6. Monthly percentage biomass of phytoplankton groups in Lake Powell.

and cryptomonads.

Two hundred and nineteen phytoplankton species were identified in Lake Powell (Appendix A). The phytoplankton community is characterized by many species and a wide range of cell sizes. Phytoflagellates were the most common group in Lake Powell. Those species present in a large percentage of samples were Chrysochromulina parva Lackey, Rhodomonas minuta Skuja, and Cryptomonas erosa Ehreng. R. minuta was identified in every sample examined while C. parva occurred in 98 percent of all samples (Table 12). These two species had not been previously reported from Lake Powell. Other species found in more than 70 percent of the samples include Oocystis gigas var. incrassata W. and G. S. West, Ceratium hirundinella (Mueller) Schrank (forms furcoides , scotticum, and piburgense), Katablepharis ovalis Skuja, and Fragilaria crotonensis Kitton.

Important phytoplankton species during spring (March-May) were C. erosa, Cyclotella bodanica var. michiganensis Skv., R. minuta, F. crotonensis, and C. hirundinella (Table 13). C. erosa had 12 occurrences with greater than 10 percent biomass, 6 of which were also greater than 25 percent. C. hirundinella biomass was greater than 5 percent in 14 of the 17 spring samples. Peridinium willei was abundant at Hite and Hall's Crossing during May. C. bodanica var. michiganensis was more common in the lower conductivity down-lake stations at Oak Canyon and Wahweap Bay during April.

Dinoflagellates were common during summer (June-September) including Peridinium elpatiewskyi, Peridinium cunningtonii, Peridinium bipes var. tabulatum, Peridinium willei, and Ceratium hirundinella

Table 12. Selected phytoplankton species in Lakes Powell, Mead, Mohave, and Havasu and percentage occurrence of each taxon.

Taxon	Powell n=55	Mead n=45	Mohave n=30	Havasu n=29
CHLOROPHYTA				
Oocystis gigas var. *incrassata*	72.7%	82.2%	66.7%	79.3%
Platymonas elliptica	27.3	44.4	40.0	37.9
PYRRHOPHYTA				
Glenodinium gymnodinium var. *biscutelliforme*	30.9	20.0	23.3	34.5
Gymnodinium helveticum	25.4	20.2	30.0	13.8
Ceratuim hirundinella	87.3	88.9	60.0	72.4
CRYPTOPHYTA				
Rhodomonas minuta	100.0	100.0	100.0	100.0
Cryptomonas erosa	94.5	80.0	56.7	62.1
C. marssonii	41.8	73.3	90.0	93.1
C. erosa var. *reflexa*	7.3	22.2	3.3	0.0
Katablepharis ovalis	81.8	86.7	83.3	86.2

(continued)

Table 12. (Continued)

Taxon	Powell n=55	Mead n=45	Mohave n=30	Havasu n=29
CHRYSOPHYCEAE				
Chrysochromulina parva	98.2	97.8	100.0	100.0
Mallomonas pseudocoronata	52.7	28.9	36.7	31.0
Dinobryon divergens	61.8	48.9	76.7	72.4
BACILLARIOPHYCEAE				
Synedra ulna	21.8	42.2	70.0	31.0
S. radians	41.8	26.7	70.0	82.8
Cyclotella bodanica var. *michiganensis*	38.2	13.3	0.0	0.0
C. atomus (<11 um)	25.5	8.9	26.7	24.1
C. michiganiana (<11 um)	67.3	55.6	0.0	3.4
C. pseudostelligera	38.2	35.6	56.7	62.1
C. meneghiniana (<11 um)	18.2	11.1	20.0	44.8
Fragilaria crotonensis	74.6	57.8	66.7	41.4
Anomoeoneis vitrea	54.6	42.2	53.3	48.3
CYANOPHYTA				
Oscillatoria limnetica	40.0	22.2	36.7	58.6
Raphidiopsis curvata	5.4	6.7	40.0	44.8

Table 13. Lake Powell phytoplankton species and size composition. Numbers represent the number of occurrences in each season where the species contributed more than 5, 10, 25, or 50% of total biomass.

	Spring				Summer				Fall				Winter			
	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50
<5 um																
Chrysochromulina parva Lackey	1	2			6	3			1				3			
>5<11 um																
Katablepharis ovalis Skuja									1							
Rhodomonas minuta Skuja	5	1			3	2							4	3		
Ochromonas minuscula Conrad					1											
Pseudokephyion sp.													1			
Pseudopedinella erkensis Skuja													1			
Cyclotella atomus Hust.														1		
C. michiganiana Skv.										2		1				
Unidentified flagellates					1	1								1		
>11 um <21 um																
Platymonas elliptica G. M. Smith									1							
Glenodinium armatum Levander					1											
Cryptomonas marssonii Skuja									1				1			
C. brevis Schiller										1						
C. pyrenoidifera Skuja	1				2	1										
Cyclotella michiganiana						1			1				1			
Stepanodiscus astraea var. *minutula* (Kutz.) Grun.		1					1							1		
Unidentified phytoflagellates									1							

(continued)

Table 13. (Continued)

	Spring >5	Spring >10	Spring >25	Spring >50	Summer >5	Summer >10	Summer >25	Summer >50	Fall >5	Fall >10	Fall >25	Fall >50	Winter >5	Winter >10	Winter >25	Winter >50
>21 um <44 um																
Oocystis gigas var. incrassata					2	1										
Cosmarium candianum f. minutum Compere	1	1														
Scenedesmus bijuga (Turp.) Lagerheim.					1											
S. dimorphus (Turp.) Kutz.					1											
Sphaerocystis schroeteri Chodat	1				1											
G. ubberimum var. rotundatum (Klebs) Popovsky					3											
Peridinium bipes var. tabulatum (Ehrenberg) LeFevre						2	3				1					
P. cunningtonii Lemm.					1	1		1								
P. elpatiewskyi (Ostenfeld) Lemm.					5	6	1		1							
P. quadridens Stein						2										
Cryptomonas erosa Ehrenberg.	2	6	6		10	4			1	2				1	6	3
C. erosa var. reflexa Marsson	1	1														
C. parapyrenoidifera Skuja					2											
C. pyrenoidifera Geitler	1															
Mallomonas pseudocoronata Prescott		1														
Anomoeoneis vitrea (Grun.) Ross					3	1	1			1						
Cyclotella bodanica var. michiganensis Skv.	3	2	2	1	1				1				1			
N. tripunctata (Mull.) Bory.													1			
S. astraea var. minutula													1			
Synedra radians Kutz.						2										

(continued)

Table 13. (Continued)

	Spring				Summer				Fall				Winter			
	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50
>44<64 um																
Oocystis gigas var. incrassata W. and G. S. West	3	1	3													
Staurastrum sp.									2	1						
Diplopsalis acuta Entz.					2											
Peridinium willei Huitfeldt-Kaas	2	2				2										
Cryptomonas rostotiformis Skuja		1														
Dinobryon divergens Imhof					1	1										
Synedra radians					1	1										
Chroococcus limneticus Lemm.					3	1	2	2								
>64 um																
Ceratium hirundinella (Mueller) Schrank	6	6	1	1	2	3	1		1				2	3	1	
Asteronella formosa Hass.													1			
Fragilaria crotonesis Kitt.	2		4	1		1							2		5	1
Synedra radians					1				2							
S. ulna (Nitz.) Ehr.									1			2				
Anabaena minderi Hub.-Pest.					1											

(Table 13). Other common species were Anomoeoneis vitrea, Chrysochromulina parva, and Rhodomonas minuta. Peridinium elpatiewskyi was common in August at all stations while Peridinium bipes var. tabulatum increased in relative abundance down-lake during September.

The most common species during fall (October-November) were Synedra ulna, Cyclotella michiganiana, and Cryptomonas erosa (Table 13). S. ulna contributed greater than 65 percent total biomass at Zahn Bay and Wahweap Bay during October.

The commonly occurring species during winter (December-February) were Rhodomonas minuta, Cryptomonas erosa, Fragilaria crotonensis, and Ceratium hirundinella (Table 13). Cyclotella michiganiana was observed in greater abundance in Wahweap Bay. The species composition at the other stations was similar.

Lake Mead

Phytoplankton biomass in Lake Mead was highest in Middle Las Vegas Bay where concentrations averaged 1.12 g/m^3 during the study (Table 14). Biomass was extremely low in the up-lake stations where concentrations were 3-4 times lower at each of Gregg, Virgin, and Boulder Basins than at Middle Las Vegas Bay. Seasonal and annual phytoplankton biomass was similar among Gregg, Virgin, and Boulder Basins.

Lake Mead seasonal biomass patterns for the four stations sampled are presented in Fig. 7. Lake-wide annual biomass ranged from 0.16 g/m^3 in November and January to 1.1 g/m^3 in July. Biomass was

Table 14. Seasonal mean phytoplankton biomass and percentage biomass by size in Lake Mead stations from March 1981 to February 1982.

	Phytoplankton biomass (g/m^3)	Percentage biomass by size (um)					
		<5	>5<11	>11<21	>21<44	>44<64	>64
Temple - Gregg Basin							
Spring	0.139	2.2	7.6	10.3	50.0	2.4	27.7
Summer	0.356	5.0	22.4	16.5	29.0	2.4	24.7
Fall	0.670	3.5	4.7	5.8	11.3	2.6	72.2
Winter	0.196	9.1	15.8	9.3	41.4	4.4	20.0
Mean	0.325	4.6	13.3	10.9	26.1	2.7	42.3
Virgin Basin							
Spring	0.123	3.5	7.3	19.9	44.2	8.2	16.8
Summer	0.202	2.3	33.1	12.2	37.0	1.1	14.1
Fall	0.740	1.7	5.0	2.7	6.9	0.7	83.0
Winter	0.196	10.9	31.5	5.0	30.3	1.6	20.9
Mean	0.277	3.3	16.1	7.6	22.4	1.8	48.7
Boulder Basin							
Spring	0.116	6.4	8.7	46.2	17.6	14.4	6.6
Summer	0.418	3.9	17.9	6.7	17.5	15.5	38.6
Fall	0.383	1.9	6.6	4.2	11.2	13.8	62.3
Winter	0.222	7.4	20.2	4.2	58.7	5.1	4.5
Mean	0.293	4.2	14.6	10.0	21.7	13.5	36.0
Middle Las Vegas Bay							
Spring	1.199	5.8	4.4	28.8	20.5	8.6	31.9
Summer	2.081	2.9	11.1	11.6	25.5	0.3	48.6
Fall	0.534	2.7	6.3	7.6	28.2	11.7	43.6
Winter	0.144	10.8	23.2	5.1	44.9	2.8	13.3
Mean	1.118	3.9	9.3	15.7	25.0	3.5	42.6

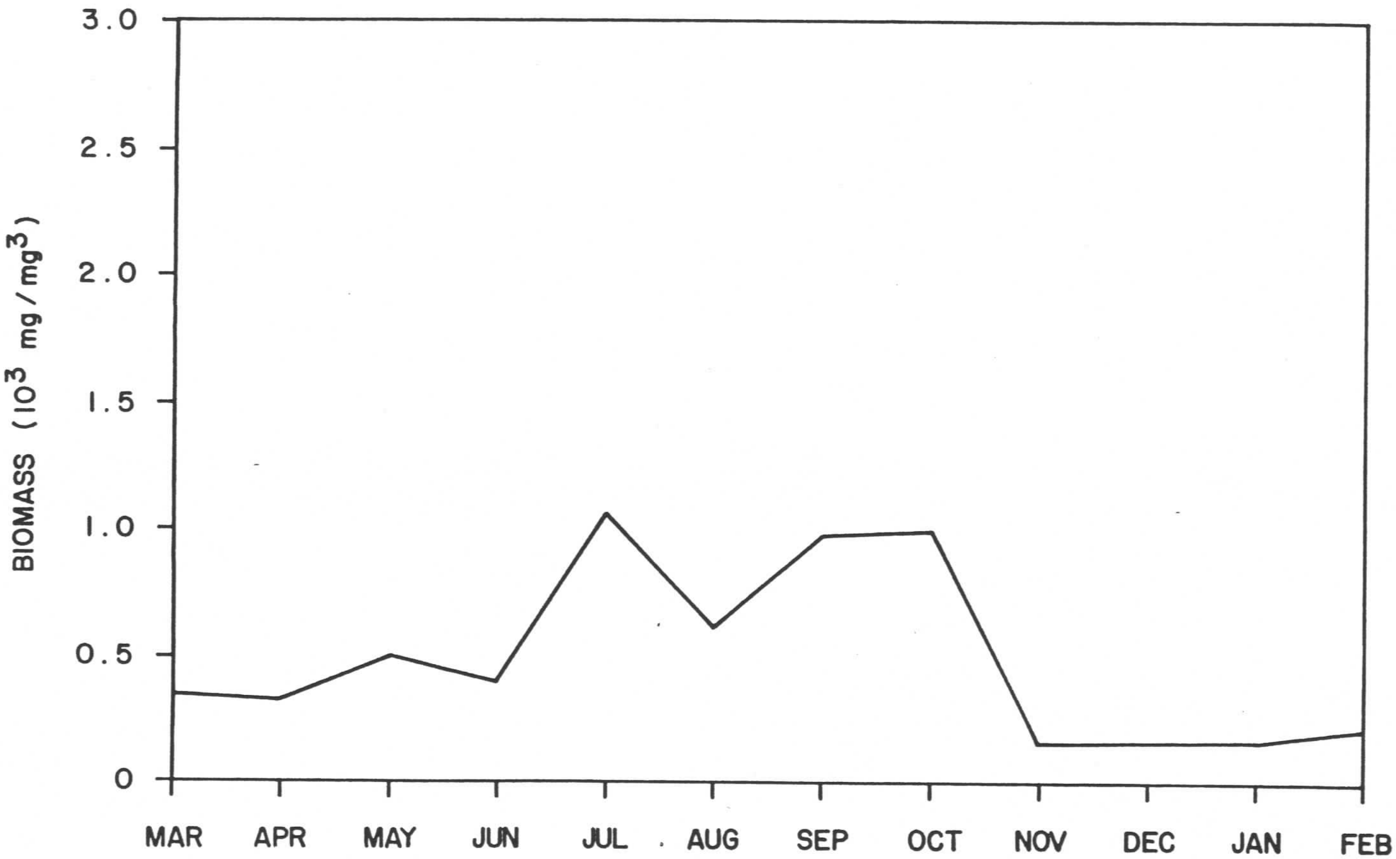

Figure 7. Monthly phytoplankton biomass in Lake Mead.

low from March to June followed by increases to 1.1 g/m^3 in July. Biomass remained at nearly 1.0 g/m^3 throughout the summer months and October except in August when the concentration was slightly lower. During November and the remainder of winter biomass was low (0.2 g/m^3). Annual lake-wide mean biomass was 0.52 g/m^3 during the study. Areal weighting of phytoplankton biomass reduced the total mean value to 0.34 g/m^3 due to the small area and large contribution of Middle Las Vegas Bay to total Lake Mead biomass.

Cryptomonads and diatoms were quantitatively the most abundant phytoplankton taxonomic groups present in Lake Mead with contributions of 34% and 30% of total lake-wide biomass. Greens (14%) and dinoflagellates (12%) were less abundant. Blue-greens and chrysomonads provided minor contributions to total annual biomass.

Succession patterns of taxonomic groups in Lake Mead are shown in Fig. 8. Cryptomonads were dominant in November-March contributing 60-70 percent of monthly lake biomass. Greens exhibited biomass peaks in April and June. Diatoms were the dominant group throughout the summer months and into October.

Two hundred and four species were identified in Lake Mead (Appendix A). The most commonly occurring species were *Rhodomonas minuta*, *Chrysochromulina parva*, and *Ceratium hirundinella*. *R. minuta* was present in every sample, while *C. parva*, and *C. hiundinella* were found in 98% and 89% of all samples, respectively (Table 12). Other commonly occuring species which were observed in greater than 70% of the samples were *Cryptomonas erosa*, *Oocystis gigas* var. *incrassata*, *Cryptomonas marssonii*, and *Katablepharis ovalis* Skuja.

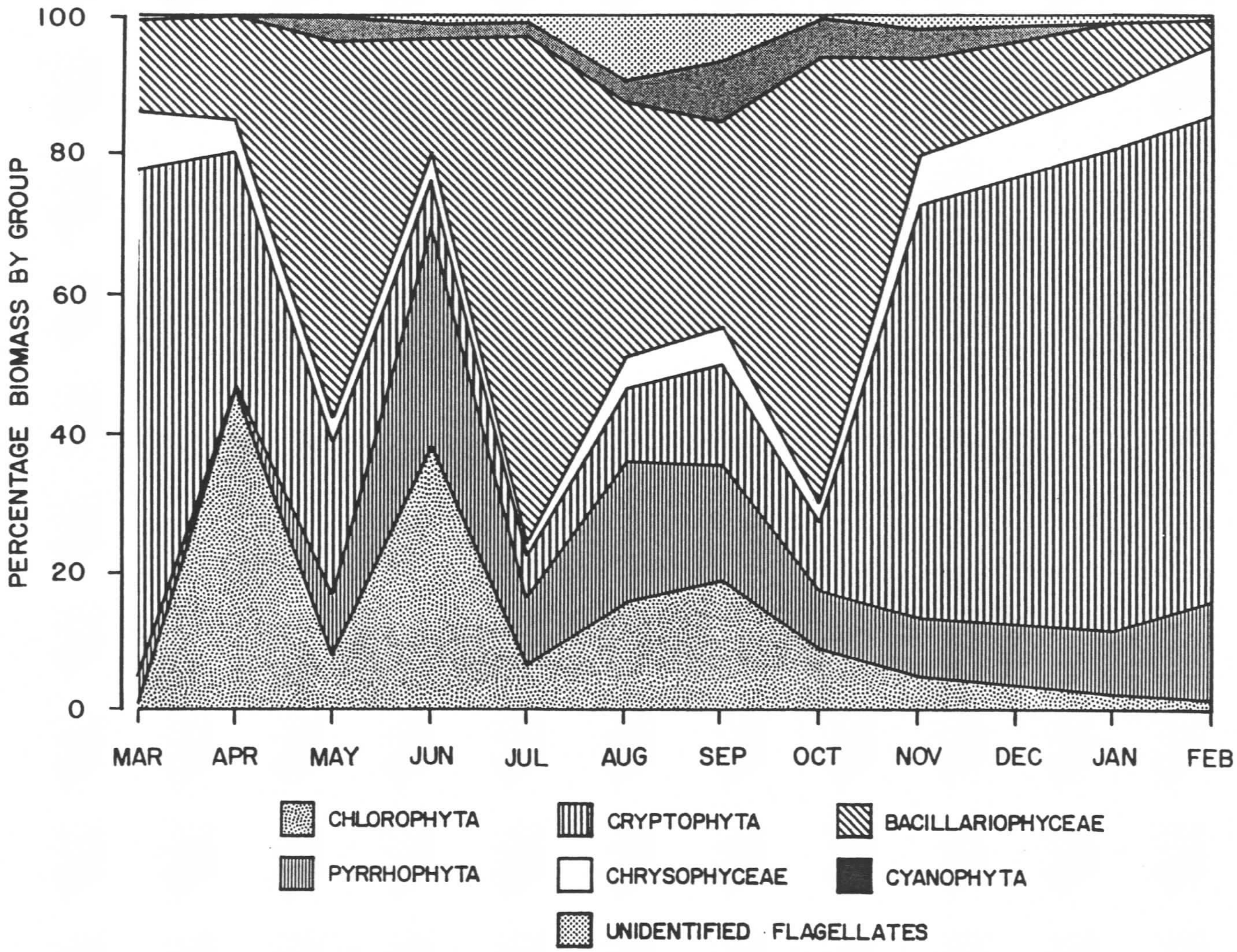

Figure 8. Monthly percentage biomass of phytoplankton groups in Lake Mead.

The species contributing the greatest biomass on a lake-wide annual basis were Synedra ulna, 23% of total biomass, Anomoeoneis vitrea, 16%, and C. erosa, 9%.

Species common during spring were Cryptomonas erosa, Rhodomonas minuta, Cryptomonas erosa var. reflexa, Chrysochromulina parva, and Sphaerocystis schroeteri (Table 15). During June-September the common species were Rhodomonas minuta, Cyclotella michiganiana, Cryptomonas erosa, Anomoeoneis vitrea, Planctonema lauterbornii, Ceratium hirundinella, Synedra ulna, and Lyngbya birgei.

Species occurring in high abundance during fall (October-November) were Rhodomonas minuta, Peridinium bipes var. tabulatum, and Synedra ulna. Common winter species were Chrysochromulina parva, Rhodomonas minuta, Cryptomonas erosa, and Ceratium hirundinella.

Lake Mohave

Phytoplankton biomass in Lake Mohave was highest at Eldorado Canyon, the most up-lake station, where concentrations averaged 1.5 g/m^3 during the study (Table 16). Biomass decreased down-lake where values were 2-2.5 times lower at Cottonwood Basin and Katherine's Landing than at Eldorado Canyon.

Monthly biomass at the three Lake Mohave stations sampled is presented in Fig. 9. Lake-wide biomass ranged from 0.3 g/m^3 during spring to 2.7 g/m^3 in October. Total biomass was low during spring and winter, increased throughout the summer months and reached a maximum in October. Biomass then decreased and remained low throughout the

Table 15. Lake Mead phytoplankton species and size composition. Numbers represent the number of occurrences in each season where the species contributed more than 5, 10, 25, or 50% of total biomass.

	Spring				Summer				Fall				Winter			
	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50
<5 um																
Chrysochromulina parva Lackey	3	3			2								5			
Cyclotella pseudostelligera Hust.													2			
Unidentified phytoflagellates		1														
>5<11 um																
Golenkinia radiata (Chod.) Wille					1											
Gymnodinium ordinatum Skuja	1															
Rhodomonas minuta Skuja	2	2	1		2	2			4				2	6	1	
Pseudokephyion sp.	1															
Pseudopedinella erkensis Skuja					1											
Cyclotella michiganiana Skv.						3	1		1	1						
Unidentified flagellates						1										
>11<21 um																
Platymonas elliptica G. M. Smith										1						
Chlamydomonas orbicularis Pringsh.			1													
Glenodinium armatum Levander					1	1										
G. pulvisulus Stein					1											
Cryptomonas erosa var. *reflexa* Marsson		2		2												
C. marssonii Skuja					2								2			
Rhodomonas lens Pasch. and Rutt.													1			

(continued)

Table 15 . (Continued)

	Spring				Summer				Fall				Winter			
	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50
Chrysococcus heverlensis Conrad					1	1										
Stephanodiscus astraea var. *minutula* (Skv.) Kutz.	1															
Unidentified phytoflagellates		1			1	1										
>21<44 um																
Oocystis parva West and West						1										
Pandorina morum (Muell.) Bory.					1											
Sphaerocystis schroeteri Chodat					2	1										
Glenodinium ambiguum Thompson									1							
G. gymnodinium var. *biscutelliforme*					1											
Peridinium bipes var. *tabulatum* (Ehrenberg) LeFevre					1		1		1	2						
P.elpatiewskyi (Ostenfeld) Lemm.					1	1	1									
P. quadridens Stein						1										
Cryptomonas sp.													1			
C. erosa Ehrenberg	2	3	5	1	4	1	1		1	1			1	1	5	2
C. tetrapyrenoidifera Skuja		1														
Mallomonas pseudocoronata Prescott						1										
Anomoeoneis vitrea (Grun.) Ross	1				1	2	1									
Cyclotella bodanica var. *michiganensis* Skv.						2										
Cymbella cistula (Ehr.) Kirchn.		1	1													
Navicula radiosa var. *tenella* (Breb. ex. Kutz.) Grun	1															
Nitzschia sp.									1							
Aphanocapsa elachista var. *conferta* West and West					1											

(continued)

Table 15. (Continued)

	Spring				Summer				Fall				Winter			
	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50
>44<64 um																
Ankyra judayi G. M. Smith	1	1														
Oocystis gigas var. incrassata West and West									1	1						
Sphaerocystis schroeteri	1	1		1												
Cryptomonas rostotiformis	1	1			1											
Dinobryon divergens Imhof					1											
Nitzschia gracilis Hantzsch.					1											
>64 um																
Planctonema lauterbornii Schmidle					2	1	1									
Ceratium hirundinella (Mueller) Schrank	3	3			3	4			2	1			7	1		
Amphipleura pellucida	1															
Asteronella formosa Hass.					1											
Fragilaria crotonesis Kitt.					1			1		1		1		1	1	
Melosira granulata var. angustissima O. M.					1											
M. varians Ag.	1															
Nitzschia denticula		1														
N. gracilis										1						
Synedra acus Kutz.									1							
S. filiformis var. exilis Cl.-Eul.													1			
S. ulna (Nitz.) Ehr.	1				1	1	1	1		1	1	2				
Stenopterobia pelagica Hust.	2															
Lyngbya birgei G. M. Smith						4			2	1			1			
Raphidiopsis curvata									1							

Table 16. Seasonal mean phytoplankton biomass and percentage biomass by size in Lake Mohave stations from March 1981 to February 1982.

	Phytoplankton biomass (g/m^3)	Percentage biomass by size (um)					
		<5	>5<11	>11<21	>21<44	>44<64	>64
Eldorado Canyon							
Spring	0.251	48.6	2.5	9.9	9.9	0.8	28.3
Summer	2.081	2.2	15.7	17.3	53.8	2.0	9.0
Fall	2.940	4.4	10.4	7.9	61.6	4.4	11.2
Winter	0.460	28.6	27.4	0.5	18.1	10.1	15.3
Mean	1.542	6.1	13.4	12.8	53.6	3.1	11.0
Cottonwood Basin							
Spring	0.304	6.5	12.7	19.6	27.4	6.0	27.8
Summer	0.757	2.6	7.9	10.8	41.4	12.1	25.5
Fall	1.470	7.6	22.7	14.5	31.2	5.3	18.6
Winter	0.290	3.5	17.9	12.2	35.2	6.9	24.3
Mean	0.717	5.2	15.0	13.5	35.1	8.3	22.9
Katherine's Landing							
Spring	0.291	3.9	12.8	14.9	44.6	6.1	17.7
Summer	0.535	5.3	10.1	11.9	43.0	1.3	28.5
Fall	1.562	5.8	16.2	24.9	24.6	21.0	7.4
Winter	0.440	3.2	24.7	18.2	33.9	2.0	18.1
Mean	0.576	5.2	14.3	18.9	33.9	11.4	16.4

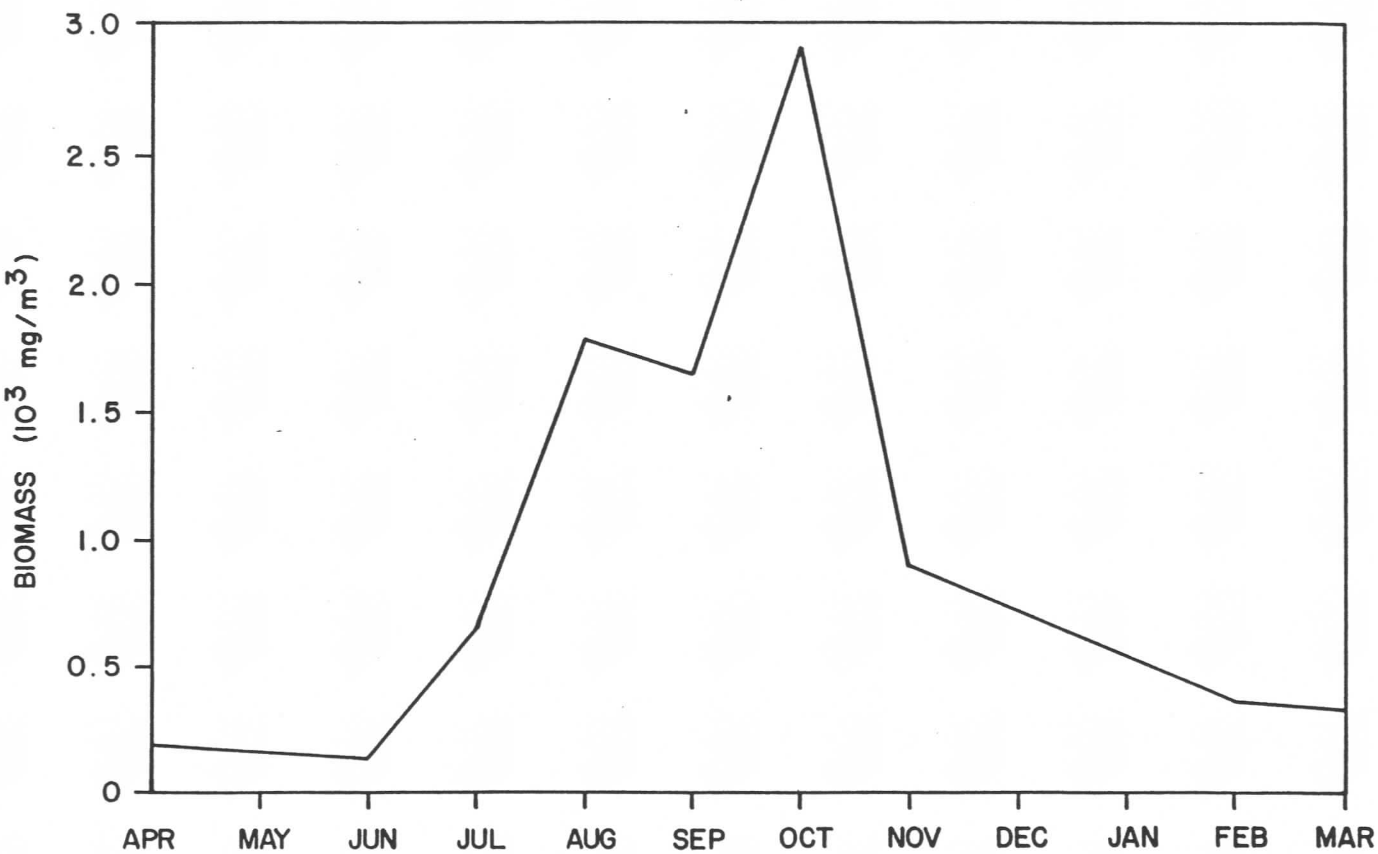

Figure 9. Monthly phytoplankton biomass in Lake Mohave.

winter and spring. Annual mean Lake Mohave biomass was 0.97 g/m^3 and the areal weighted mean was 0.78 g/m^3.

Cryptomonads, dinoflagellates and diatoms were quantitatively the most important phytoplankton groups in Lake Mohave, contributing 23, 22, and 22 percent of total lake-wide biomass, respectively. The phytoflagellates contributed more than half of the total biomass. Other taxonomic groups, in order of decreasing biomass contributions, were greens, chrysophytes, and blue-greens.

Seasonal succession of phytoplankton group composition showed diatoms as the main biomass component during spring with cryptomonads second in importance (Fig. 10). During summer (June-September) dinoflagellates were most abundant, with cryptomonads, diatoms, and blue-greens also well represented. Dinoflagellates continued their importance in October. The main components of the winter community were cryptomonads, diatoms, and greens.

One hundred and ninety four species were identified in Lake Mohave during this study (Appendix A). The most commonly occurring species were *Rhodomonas minuta* and *Chrysochromulina parva* which were present in 100% of the samples examined (Table 12). Other species present in more than 60% of the samples were *Cryptomonas marssonii*, *Ceratium hirundinella*, *Oocystis gigas* var. *incrassata*, *Dinobryon divergens*, and the diatoms, *Synedra ulna*, and *Synedra radians*. Species contributing the greatest biomass on a lake-wide annual basis were *Peridinium cunningtonii* (11%), *Rhodomonas minuta* (7%), *Raphidiopsis curvata* (7%), *Peridinium quadridens* (5%), *Cryptomonas erosa* (4%), and *Chrysochromulina parva* (4%).

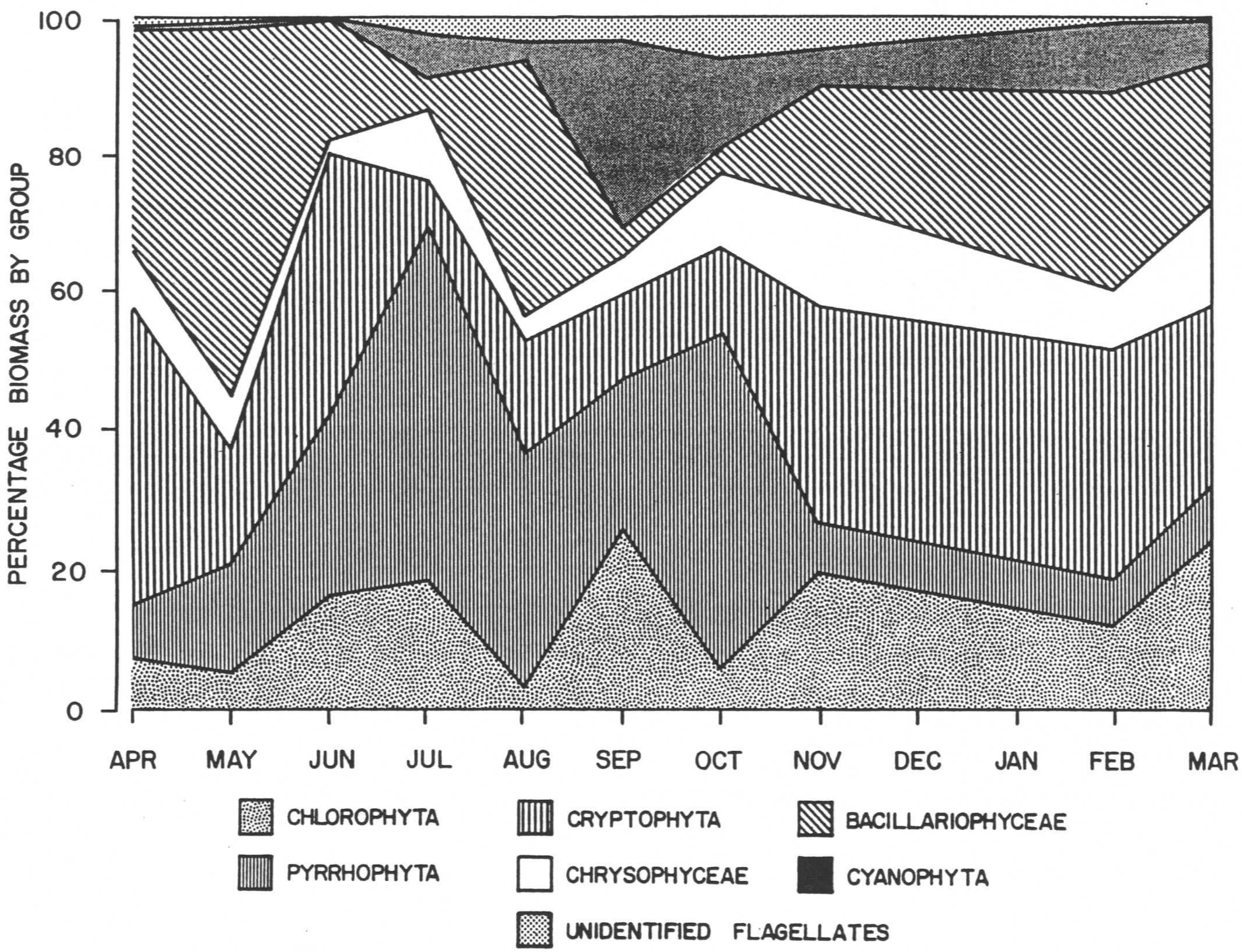

Figure 10. Monthly percentage biomass of phytoplankton groups in Lake Mohave.

The most abundant species during March-May were *Chrysochromulina parva*, *Rhodomonas minuta*, *Cryptomonas erosa*, *Cyclotella pseudostelligera*, *Diopolsalis acuta*, and *Cryptomonas marssonii* (Table 17). The species of greatest quantitative importance during June-September were *Rhodomonas minuta*, *Cryptomonas erosa*, *Anomoeoneis vitrea*, *Raphidiopsis curvata*, *Glenodinium pulvisculus*, and *Peridinium cunningtonii*. The common species in the October-November phytoplankton community were *Chrysochromulina parva*, *Rhodomonas minuta*, *Peridinium cunningtonii*, *Cryptomonas* spp., and *Raphidiopsis curvata*. The winter phytoplankton community was dominated by *Rhodomonas minuta*, *Glenodinium pulvisculus*, *Cryptomonas* spp., and *Oscillatoria tenuis*.

Lake Havasu

Lake Havasu phytoplankton biomass was highest at Upper Lake Havasu, the station closest to Davis Dam, where values averaged 1.6 g/m^3 during the study (Table 18). Biomass was lower at Havasu City and Parker Dam, where average values at each station were one-half those at Upper Lake Havasu.

Monthly total biomass for the three stations sampled in Lake Havasu is presented in Fig. 11. Lake-wide monthly biomass ranged from 0.1 g/m^3 in June to 2.9 g/m^3 in October. Seasonal succession of biomass was low during April-June, followed by rapidly increasing biomass in July and August. The single biomass maximum occurred in October which was followed by low values throughout the winter months.

Cryptomonads and diatoms were quantitatively the most important

Table 17. Lake Mohave phytoplankton species and size composition. Numbers represent the number of occurrences in each season where the species contributed more than 5, 10, 25, or 50% of total biomass.

	Spring				Summer				Fall				Winter			
	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50
<5 um																
Chrysochromulina parva Lackey	2	1			2	1			3							
Cyclotella atomus Hust.				1	1											
C. pseudostelligera Hust.														1		
>5<11 um																
Rhodomonas minuta Skuja	1	5			5	3			3				1	2		
C. pseudostelligera Hust.														1		
Unidentified flagellates									1							
>11<21 um																
Glenodinium armatum Levander					1											
G. pulvisulus Stein					3								2			
C. marssonii Skuja	1	2			1											
S. astraea var. minutula	2				1				1							
Dactylococcopsis irregularis G. M. Smith									1							
Unidentified phytoflagellates					1				1							

(continued)

Table 17 . (Continued)

	Spring >5	Spring >10	Spring >25	Spring >50	Summer >5	Summer >10	Summer >25	Summer >50	Fall >5	Fall >10	Fall >25	Fall >50	Winter >5	Winter >10	Winter >25	Winter >50
>21<44 um																
Coelastrum sphaericum Naegeli						1				1						
Cosmarium candianum f. minutum Compere	1															
Oocystis lacustris Chodat		1	1										1	1		
Pandorina morum (Muell.) Bory.						1			1							
Sphaerocystis schroeteri Chodat						1	1									
Diplopsalis acuta Entz.	3				1											
Glenodinium ambiguum Thompson					1	1										
G. ubberimum var. rotundatum (Klebs) Popovsky	1									1						
P. cunningtonii Lemm.					1		1		2		1					
P.elpatiewskyi (Ostenfeld) Lemm.					2	1										
P. quadridens Stein					1		1			1						
Cryptomonas sp.									3	1					1	
C. erosa Ehrenberg	2	1	1		2	2	1			1				2		
C. reflexa Skuja		2														
Anomoeoneis vitrea (Grun.) Ross						2	1	1								
Cocconeis placentula var. euglypta (Ehrenberg) Cleve	1				1	1										
N. tripunctata (Mull.) Bory.	1															
Synedra radians					2		1									
Chroococcus limneticus Lemm.						2										

(continued)

Table 17 . (Continued)

	Spring >5	>10	>25	>50	Summer >5	>10	>25	>50	Fall >5	>10	>25	>50	Winter >5	>10	>25	>50
>44<64 um																
Oocystis gigas var. incrassata W. and G. S. West	2															
Staurastrum sp.						1				1						
Cryptomonas rostotiformis Skuja	2								1							
Dinobryon divergens Imhof	2	1			1					1						
>64 um																
Ceratium hirundinella (Mueller) Schrank	2		1		1		1									
Diatoma vulgare Bory.		1	1										1			
Fragilaria crotonesis Kitt.	1	2				2										
M. varians Ag.		1	1													
Synedra radians										1			1			
S. ulna (Nitz.) Ehr.	1	2														
Anabaena minderi Hub.-Pest.					2											
Oscillatoria limnetica Lemm.					3											
O. tenuis Agardh.	2													2		
Raphidiopsis curvata					2		2		1		1					

Table 18. Seasonal mean phytoplankton biomass and percentage biomass by size in Lake Havasu stations during spring, summer, fall, and winter.

	Phytoplankton biomass (g/m^3)	Percentage biomass by size (um)					
		<5	>5<11	>11<21	>21<44	>44<64	>64
Upper Lake Havasu							
Spring	0.351	3.6	22.4	8.8	22.5	0.7	41.9
Summer	1.429	3.2	8.2	14.5	49.5	9.6	15.0
Fall	2.995	3.4	6.6	10.6	25.3	1.3	52.8
Winter	0.472	8.6	21.8	41.2	2.8	7.4	18.4
Mean	1.585	3.5	8.4	13.4	33.6	4.7	36.4
Havasu City - South							
Spring	0.289	8.6	12.2	4.8	61.6	2.6	10.2
Summer	0.945	5.3	11.6	16.3	45.2	4.6	17.0
Fall	1.237	12.8	16.3	21.4	25.0	8.4	16.1
Winter	0.281	3.5	24.1	20.2	46.3	0.9	5.2
Mean	0.740	8.1	13.7	16.8	40.4	5.5	15.5
Parker Dam							
Spring	0.164	6.5	21.1	8.0	38.1	9.3	17.0
Summer	0.912	5.7	13.0	17.8	40.3	7.3	15.9
Fall	1.489	8.9	12.5	32.3	34.2	4.1	8.0
Winter	0.354	2.8	11.1	12.1	70.0	4.0	0.1
Mean	0.712	6.8	13.4	21.9	39.2	6.2	12.5

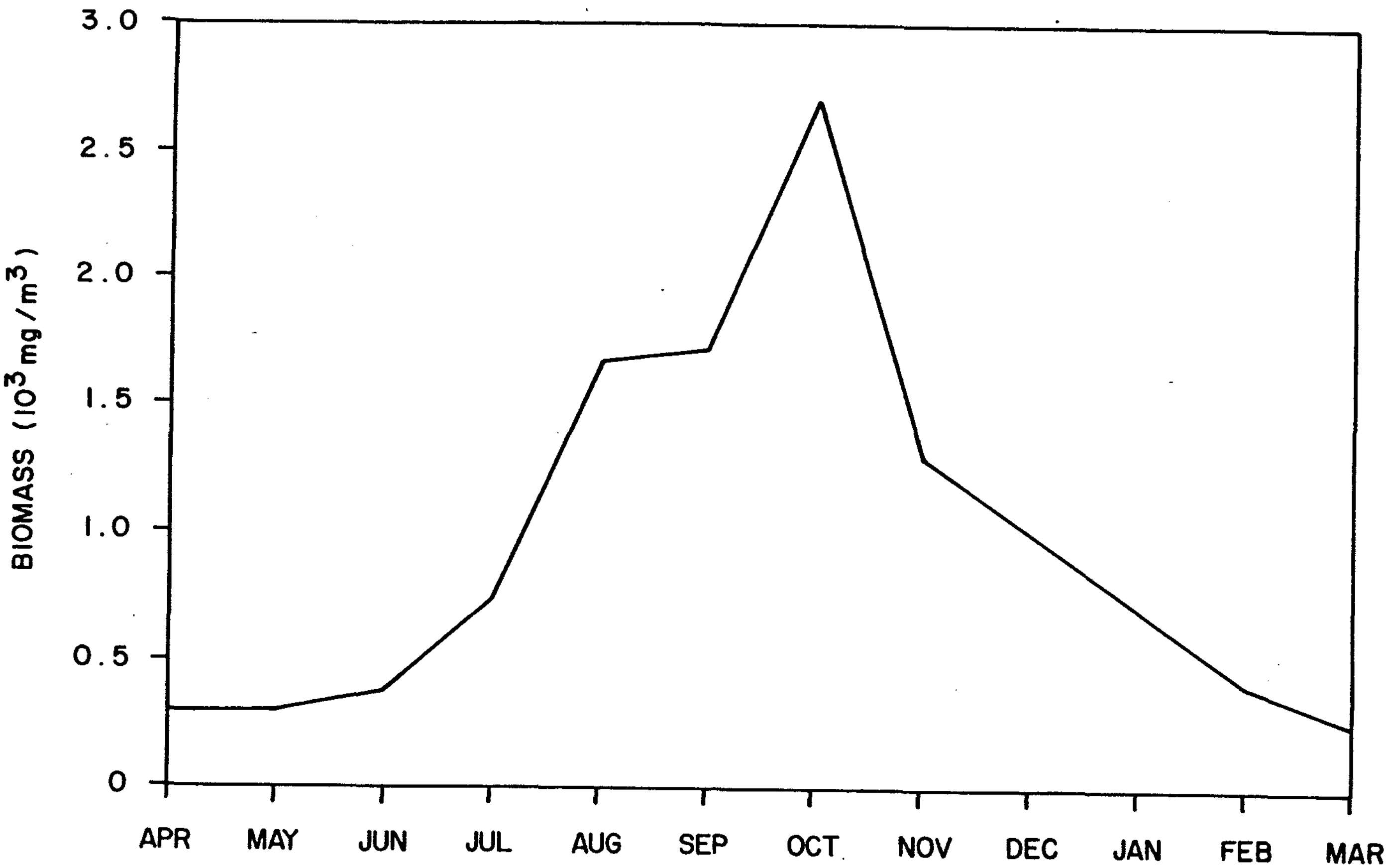

Figure 11. Monthly phytoplankton biomass in Lake Havasu.

taxonomic groups in Lake Havasu, contributing 26 and 21 percent, respectively, to total annual biomass. The remaining biomass was distributed as follows: dinoflagellates (17%), greens (14%), chrysophytes (12%), and blue-greens (7%). Phytoflagellates (dinoflagellates, cryptomonads, and chrysomonads) were quantitatively important, collectively representing 54% of total annual lake biomass.

Seasonal succession of phytoplankton taxonomic groups is presented in Fig. 12. Cryptomonads were the main component of the phytoplankton community during spring and winter and contributed lowest relative biomass in July-October. Diatoms dominated during these summer months contributing 20-40% of the total monthly biomass. Diatom biomass ranged from less than 5% in April-June to 44% in July. Blue-green biomass was low throughout the year with highest relative biomass during September and October.

One hundred and eighty-four species were identified in Lake Havasu during this study (Appendix A). The most commonly occurring species were Rhodomonas minuta and Chrysochromulina parva, found in all of the samples examined. Each taxon contributed more than 5% of total biomass in half of the samples examined (Table 19). Other species present in more than 70% of samples were Oocystis gigas var. incrassata, Ceratium hirundinella, Cryptomonas erosa, Cryptomonas marssonii, Katablepharis ovalis, Dinobryon divergens, and Synedra radians.

Species contributing greatest biomass on a lake-wide annual basis were Synedra ulna (10%), Peridinium elpatiewskyi (9%), Anomoeoneis vitrea (9%), Raphidiopsis curvata (5%), Rhodomonas minuta (4%), and Cryptomonas erosa (3%). Rhodomonas minuta and Chrysochromulina parva

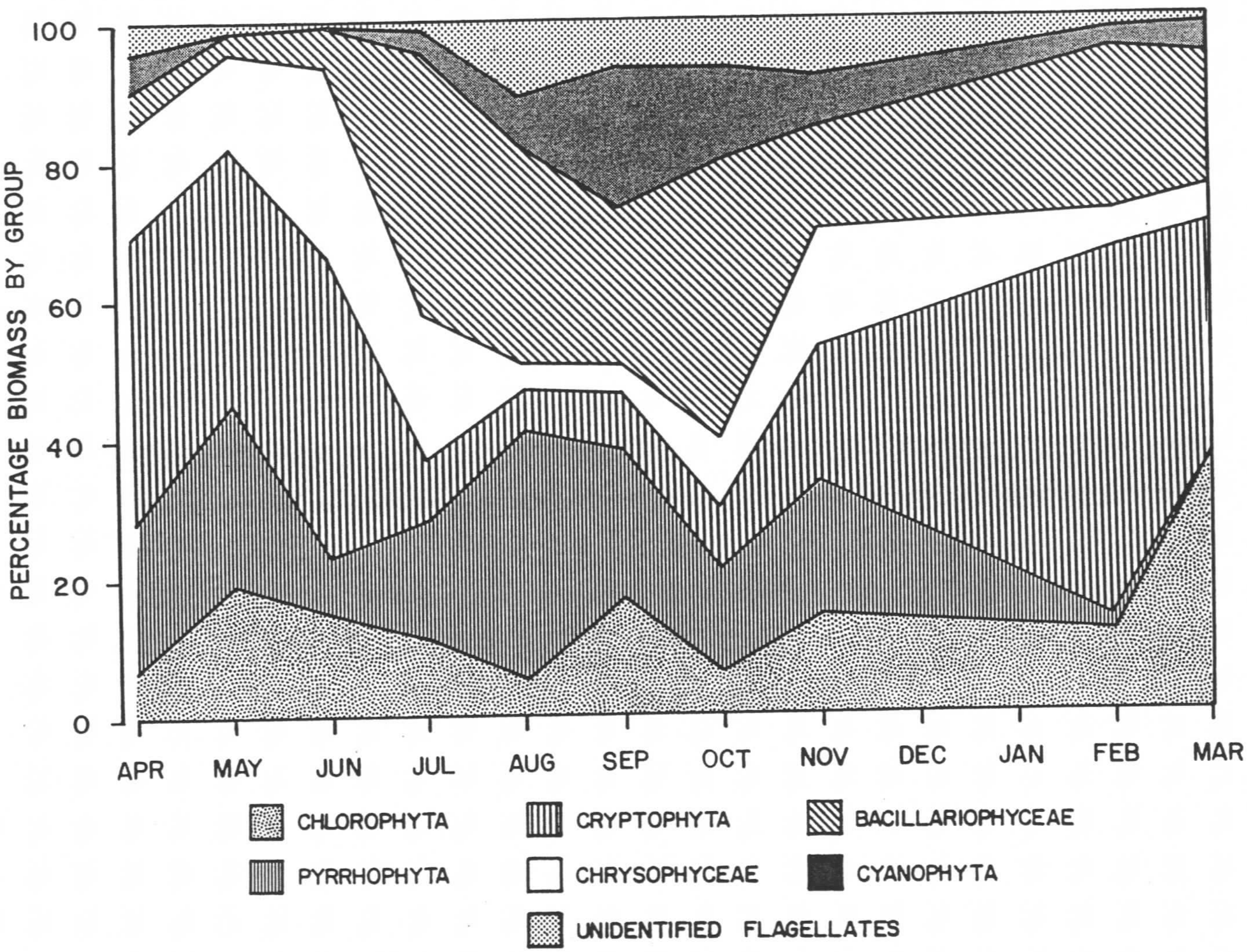

Figure 12. Monthly percentage biomass of phytoplankton groups in Lake Havasu.

Table 19. Lake Havasu phytoplankton species and size composition. Numbers represent the number of occurrences in each season where the species contributed more than 5, 10, 25, or 50% of total biomass.

	Spring				Summer				Fall				Winter			
	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50
<5 um																
Chrysochromulina parva Lackey	2	2			4	1			2	3						
>5<11 um																
Rhodomonas minuta Skuja	2	5			3	1			3				2			
Pseudopedinella erkensis Skuja					3											
Cyclotella glomerata Bachm.	1															
C. meneghiniana Kg.						1										
Stephanodiscus astraea var. minutula Kg. Grun.													1			
Unidentified flagellates	4															
>11<21 um																
Platymonas elliptica G. M. Smith									1							
Glenodinium armatum Levander					2	1										
G. pulvisulus Stein					2											
Cryptomonas ovata Ehrenberg.									1							
Cryptomonas sp.									2							
C. marssonii Skuja	3				3	1										
Cyclotella meneghiniana									1					1		
S. astraea var. minutula														1		
Unidentified phytoflagellates									2							

(continued)

Table 19 . (Continued)

	Spring				Summer				Fall				Winter			
	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50	>5	>10	>25	>50
>21<44 um																
Coelastrum sphaericum Naegeli						1										
Cosmarium candianum f. minutum Compere					1											
Dictyosphaerium pulchellum Wood									1	1						
Oocystis lacustris Chodat			2	1									1			
Sphaerocystis schroeteri Chodat					1											
Diplopsalis acuta Entz.		2														
G. ubberimum var. rotundatum (Klebs) Popovsky					1				1							
P. cunningtonii Lemm.										1						
P.elpatiewskyi (Ostenfeld) Lemm.					3	3			2	2						
P. quadridens Stein					1											
Cryptomonas erosa Ehrenberg	1	3	1		2		2							1	1	1
C. reflexa Skuja		2	1													
Mallomonas pseudocoronata Prescott										1						
Anomoeoneis vitrea (Grun.) Ross					1	5	3		1							
Navicula radiosa var. tenella (Breb. ex. Kutz.) Grun	1															
Synedra radians					1	3										
Dactylococcopsis irregularis G. M. Smith					1											

(continued)

Table 19 . (Continued)

	Spring >5	>10	>25	>50	Summer >5	>10	>25	>50	Fall >5	>10	>25	>50	Winter >5	>10	>25	>50
>44<64 um																
Staurastrum sp.					2	1			2							
Cryptomonas rostotiformis	1					1										
Dinobryon divergens Imhof							1									
Anabaenopsis elenkinii Miller					1				1							
>64 um																
Ceratium hirundinella (Mueller) Schrank	1	1	2		2	2										
Fragilaria crotonesis Kitt.			1											1		
S. ulna (Nitz.) Ehr.												1				
Anabaena minderi Hub.-Pest.						1										
Oscillatoria agardhii Gomont	1															
O. tenuis Agardh.	1															
Rapdidiopsis curvata					1	2			2	1						

were perennial species throughout this study.

Species of quantitative importance during March-May were *Cryptomonas marssonii, Oocystis lacustris, Cryptomonas erosa,* and *Ceratium hirundinella* (Table 19). Common species during June-September were *Glenodinium armatum, Pseudopedinella erkensis, Peridinium elpatiewskyi, Cryptomonas erosa, Amonoeoneis vitrea, Staurastrum* sp., *Ceratium hirundinella, Synedra radians,* and *Raphidiopsis curvata.*

Important species in the fall phytoplankton community were *Peridinium elpatiewskyi, Cryptomonas* spp., *Staurastrum* spp., *Dictyosphaerium pulchellum,* and *Raphidiopsis curvata.* The most important species during December-January were *Cryptomonas erosa, Fragilaria crotonensis, Cyclotella meneghiniana,* and *Stephanodiscus astraea* var. *minutula*.

Phytoplankton Biomass Size Structure

Lake Powell

Netplankton >64 um contributed the greatest lake-wide phytoplankton biomass in Lake Powell with an annual mean of 37% (Table 20). The second highest lake-wide biomass component was the >21<44 um size fraction which composed 34% of the total biomass. Phytoplankton <20 um contributed nearly 20%, while cells in the >44<64 um size class represented less than 10% of the biomass.

The spatial distribution of biomass >64 um in Lake Powell showed some dramatic differences (Table 11). The San Juan Arm region at Zahn

Table 20. Seasonal mean phytoplankton biomass and percentage biomass by size in lakes Powell, Mead, Mohave, and Havasu from March 1981 to February 1982.

	Phytoplankton biomass (g/m^3)	Percentage biomass by size (um)					
		<5	>5<11	>11<21	>21<44	>44<64	>64
Lake Powell							
Spring	0.753	2.2	5.2	2.6	30.2	11.5	48.3
Summer	0.898	6.4	9.3	11.4	48.6	12.0	12.3
Fall	1.725	2.1	11.4	6.0	10.9	6.2	63.5
Winter	0.370	3.7	8.8	4.3	39.1	1.5	42.7
Mean n=55	0.838	4.0	8.6	7.1	34.2	9.6	36.5
Lake Mead							
Spring	0.394	5.3	5.2	27.8	24.8	8.5	28.5
Summer	0.764	3.3	14.8	11.5	25.6	2.7	42.1
Fall	0.581	2.5	5.5	4.9	13.9	5.9	67.5
Winter	0.184	9.5	22.6	5.8	44.3	3.5	14.3
Mean n=45	0.517	4.0	11.6	13.1	24.4	4.6	42.3
Lake Mohave							
Spring	0.282	18.1	9.7	15.1	28.1	4.5	24.5
Summer	1.124	2.8	13.1	14.9	49.3	4.2	15.8
Fall	1.991	5.5	15.0	14.0	44.4	9.0	12.1
Winter	0.397	13.1	24.1	9.9	28.1	6.3	18.5
Mean n=30	0.972	5.7	14.0	14.4	44.6	6.2	15.1
Lake Havasu							
Spring	0.239	6.9	17.2	6.7	46.0	4.6	18.5
Summer	1.052	4.7	11.0	16.2	44.9	7.3	15.9
Fall	1.907	6.9	10.2	18.6	27.6	3.6	33.2
Winter	0.369	5.4	19.0	26.6	35.3	4.6	9.2
Mean n=29	0.934	5.8	11.4	17.0	37.2	5.4	23.1

Bay was dominated by the >64 um size fraction with seasonal ranges from 6 to 84% of the total station biomass and an annual mean of 62% (Table 11). Diatoms prevailed during these peaks with F. crotonensis most abundant during spring and Synedra ulna in fall (Table 13). Lower Lake Powell also showed a preponderence of netplankton size fractions. The >64 um fraction contributed 42% of the total annual biomass at Wahweap Bay. C. hirundinella was the dominant species during spring in this size fraction while S. ulna dominated during fall. In contrast to relatively high percentage contribution by the >64 um fraction at these stations, annual mean percentages of biomass at Oak Canyon and Hall's Crossing were only 20 and 28 percent, respectively (Table 11).

Seasonally, relative biomass in the >64 um fraction was highest in February (50%), March (67%), April (67%), and October (64%) (Fig. 13). The most abundant phytoplankton groups present were diatoms in April, October, and February, and dinoflagellates in March (Fig. 6).

Relative biomass in the >21<44 um ranged from 19 % at Zahn Bay to 45% at Oak Canyon with values similar at Hite, Hall's Crossing, and Wahweap Bay (Table 11). Seasonally, this size fraction was one of the main biomass components in each month except October (Fig. 13). Lake-wide annual means ranged from 18% of total biomass in March to 57% in July. The >21<44 um size was the main phytoplankton component during the summer months of July, August (47%), and September (49%) when dinoflagellates and cryptomonads were the main components of the phytoplankton community (Figs. 6, 13). The most abundant species during this period were C. erosa, Peridinium elpatiewskyi, and Peridinium bipes var. tabulatum . C. erosa contributed more than 5% total biomass in 14

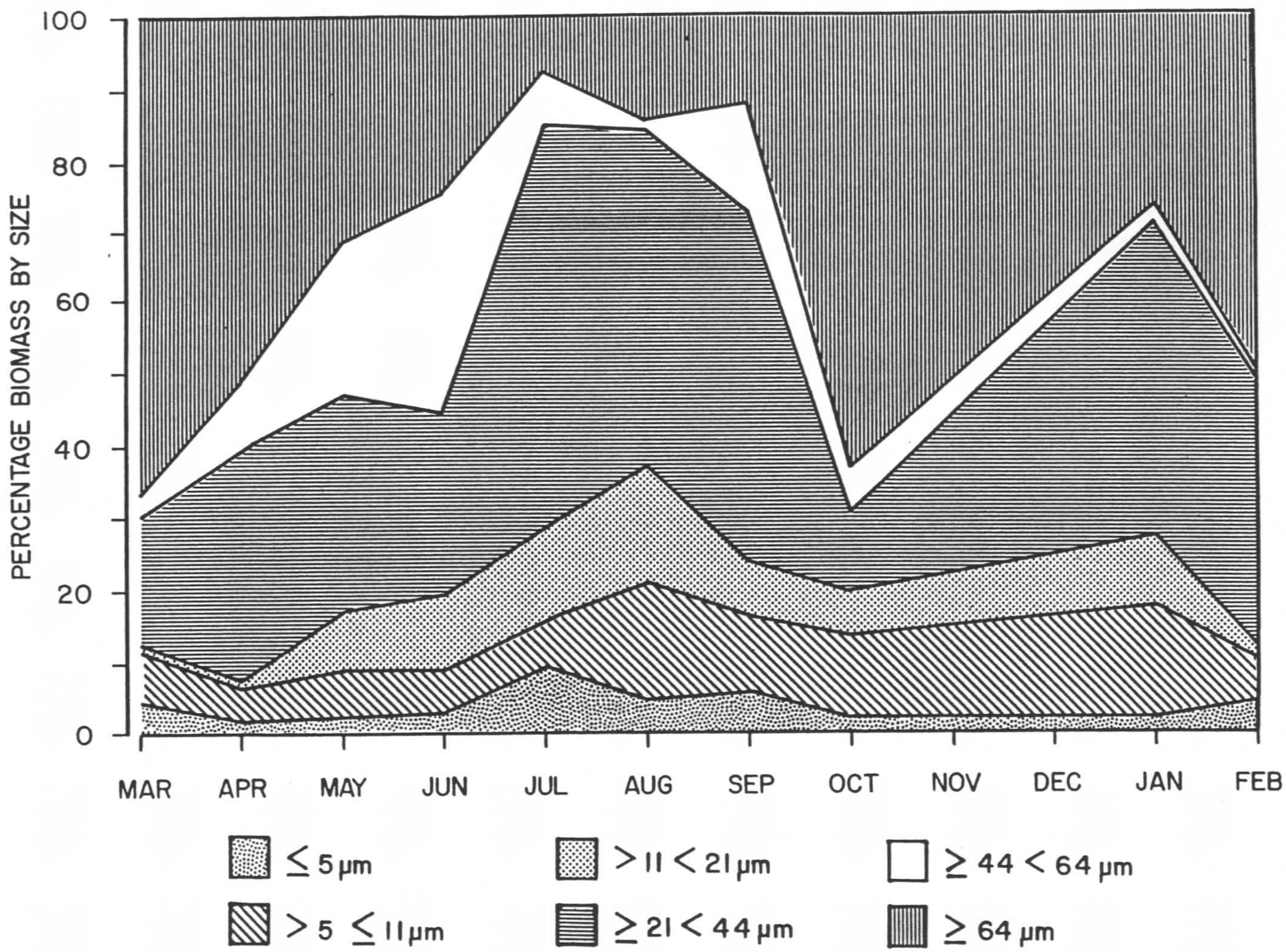

Figure 13. Monthly percentage phytoplankton biomass by size in Lake Powell.

of 21 samples while *P. elpatiewskyi* occurred in greater than 5% total biomass in 12 samples, 7 of which were also greater than 13% (Table 10).

Phytoplankton biomass in the >44<64 um size fraction was similar in Lake Powell at all stations sampled. The percentage contribution of biomass in this fraction was generally low throughout the year with highest relative abundance of 22 and 31 percent of total biomass in May and June, respectively. The most abundant algal groups were greens, dinoflagellates, and blue-greens. *Peridinium willei, Chroococcus limneticus,* and *O. gigas* var. *incrassata* were the most abundant species.

Biomass <20 um contributed nearly 20% to lake-wide annual biomass. Considering their small size and cell volume, evaluating cell abundance instead of cell volume would have increased their apparent importance considerably. Monthly biomass in these <20 um size fractions did not fluctuate greatly compared to the >64 um and >44<64 um size fractions (Fig. 13). This group comprised 37% during summer with individual fractions contributing 9% in June (<5 um), and 16% in August by each of the >5<11 um and >11<21 um fractions (Table 11). Cryptomonads, chrysomonads, and diatoms were the main components.

The <5 um phytoplankton biomass fraction was highest in July (Fig. 13), and ranged from minimum annual values of 2-1% of total biomass during spring, fall, and winter to maximum values during July (9%). Annual mean biomass fractions were similar at all stations (Table 11). *Chrysochromulina parva* was the most abundant species in this size class, occurring in 98% of the 55 samples examined and contributing

greater than 5% total biomass in 16 of the samples. Important species in the >5<11 um size fraction were *Katablepharis ovalis* Skuja, *Rhodomonas minuta,* and *Cyclotella michiganiana* Skv.

Biomass in the >11<21 um fraction showed some degree of seasonality, with highest biomass in July (13%) and August (16%) and minimum biomass during late winter and early spring. Species of greatest abundance in this fraction were *Cryptomonas* spp., *Stephanodiscus astraea* var. *minutula* and *Cyclotella michiganiana*.

Lake Mead

Netplankton >64 um were also the main component of the phytoplankton community in Lake Mead contributing 43% of the total annual lake-wide biomass (Table 20). Size fraction >21<44 um was second most abundant in Lake Mead during this study, contributing 24 percent of the annual phytoplankton biomass. Quantitatively the third most abundant phytoplankton size fraction were cells >11<21 um in length with average relative biomass of 13%. Cells <11 um contributed 16% of total biomass. The >44<64 um fraction was of minor importance to total lake biomass.

The >64 um size fraction was similar at all Lake Mead stations throughout the year with relative biomass ranging from 36 % to 49% (Table 14).

Seasonally, the highest biomass of the >64 um fraction appeared in May (60%), July (75%), and October (74%) when diatoms were the dominant algal group (Figs. 8, 14). Lowest biomass percentages were observed in

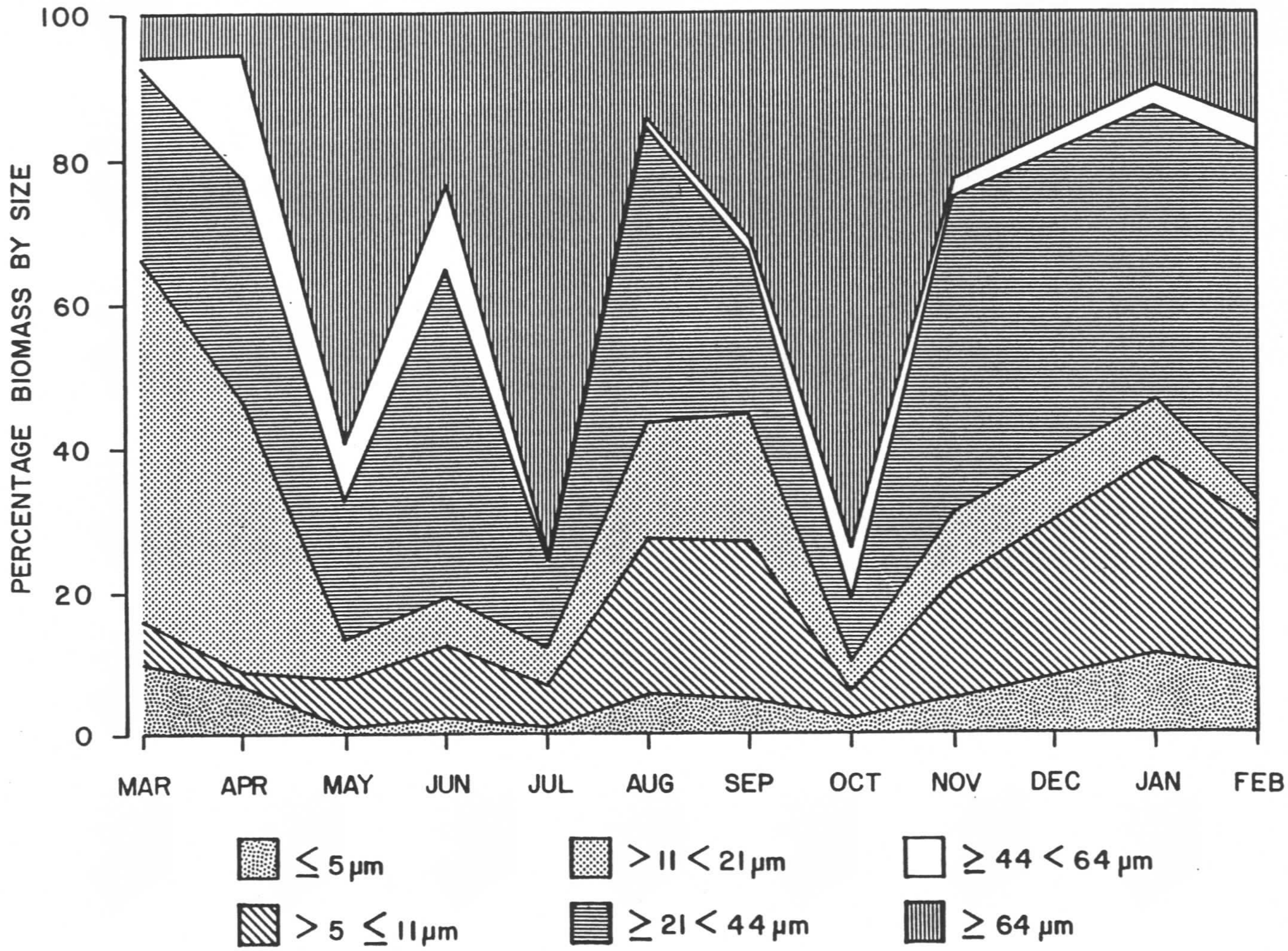

Figure 14. Monthly percentage phytoplankton biomass by size in Lake Mead.

early spring and throughout the winter months. The most common species during these >64 um biomass peaks were the diatoms Synedra ulna (May), Synedra ulna and Fragilaria crotonensis (July), and S. ulna in October.

The >21<44 um size fraction showed no large fluctations ranging from 20 to 50 percent throughout the year except for two minima in July (12%) and October (9%). The most important algal groups were greens, cryptomonads, and diatoms during the summer and cryptomonads in winter. On a lake-wide basis, the biomass of the >21<44 um size fraction was highest during spring up-lake in Gregg and Virgin Basins, 50 and 44%, respectively. This biomass fraction was high during the summer in upper Lake Mead at Virgin Basin.

Cryptomonads were the main component of the >21<44 um size fraction with Cryptomonas erosa var. reflexa and Cryptomonas marssonii the most dominant species. Relatively high fractional biomass of this size class occurred at Boulder Basin (46%) in spring, with similar values at the other three stations throughout the year.

Size fraction >5<11 um accounted for 12% of total biomass. This fraction was most important during late summer (August-September) and winter (January and February) when it contributed greater than 20% of the total biomass in each month. Small spatial differences in abundances existed throughout the year. Values ranged from 1% in July to relatively high abundances of nearly 10% in January-March (Fig. 14). In contrast to the of larger size fractions, the <5 um showed small seasonal fluctuations in relative biomass. The most abundant species in these size classes were Chrysochromulina parva and Cyclotella michiganiana (<5 um), and Rhodomonas minuta and C. michiganiana in the

>5<11 um size fraction.

Relative biomass of the >44<64 um fraction was low throughout the year with small monthly and seasonal fluctuations. On a lake-wide basis Boulder Basin had the highest values each season and an annual mean biomass of 14 percent. Common species in this size fraction were *Ankyra judayi*, *Oocustis gigas* var. *incrassata*, *Sphaerocystis schroeteri*, and *Cryptomonas rostrotiformis* (Table 15).

Lake Mohave

In contrast to the dominance of the >64 um fraction in lakes Powell and Mead, the >21<44 um size fraction was the main component of the Lake Mohave phytoplankton community, contributing 45% of annual lake-wide biomass. Average relative biomass of the size fractions >64, >11<21, and >5<11 um were nearly equal with each comprising 14-15% of total biomass (Table 20).

The >21<44 um size fraction in Lake Mohave was highest at Eldorado Canyon where biomass averaged 54% of the total (Table 16). Relative biomass of this size fraction was similar at Cottonwood Basin and Eldorado Canyon. Seasonal differences among stations were apparent with spring relative abundance increasing from up-lake Eldorado Canyon (10%) to the most down-lake location at Katherine's Landing (45%). Winter >21<44 um biomass fraction was highest at Cottonwood Basin and Katherine's Landing.

On a lake-wide basis, except during the period April-June, this size fraction was the dominant or co-dominant fraction in each month

(Fig. 15). The main taxonomic components of this fraction were dinoflagellates and cryptomonads (Figs. 10, 15).

Relative biomass in the >64 um fraction was highest in Lake Mohave at Cottonwood Basin and Katherine's Landing. Seasonally, this fraction was highest in April (25%), June (34%), September (29%), and March (30%) and lowest during July-August (3-4%) (Fig. 15). The main phytoplankton groups were diatoms and dinoflagellates with Ceratium hirundinella, Fragilaria crotonensis, and Synedra ulna the most abundant taxa (Table 17).

Collectively the three size fractions <21 um contributed one third of the total phytoplankton biomass with 6, 14, and 14% distribution by <5 um, >5<11 um, and >11<21 um size fractions, respectively.

The <5 um size fraction was most abundant during spring months. The biomass peak in May was due to high concentrations of the diatom, Cyclotella atomus at Eldorado Canyon (Fig. 15). Biomass of this fraction followed an overall low pattern but increased during the period from late summer through winter. On an annual basis the spatial distribution of biomass was fairly uniform, with Eldorado Canyon showing high percentages when total lake biomass was low. The most abundant species in this <5 um size fraction were Chrysochromulina parva, Cyclotella atomus, and Cyclotella pseudostelligera.

The distribution of the >5<11 um size class was spatially uniform throughout the year with highest seasonal values at Cottonwood Basin and Katherine's Landing (spring), Eldorado Canyon (summer), Cottonwood Basin (fall), and Eldorado Canyon (winter) (Table 16). The most important

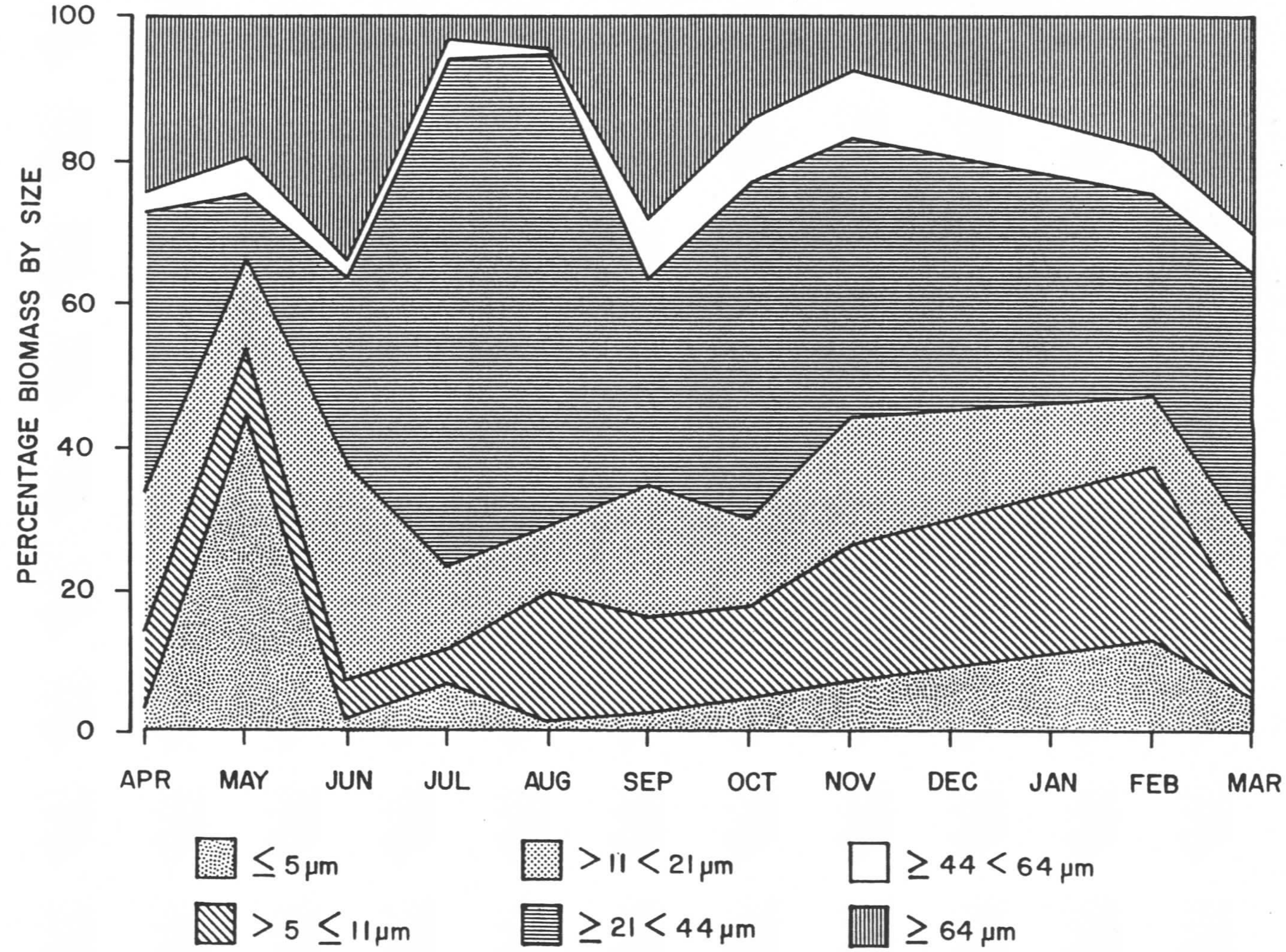

Figure 15. Monthly percentage phytoplankton biomass by size in Lake Mohave.

species in this size class were Rhodomonas minuta, and Cyclotella pseudostelligera (Table 17).

Biomass in the >11<21 um size fraction in Lake Mohave did not fluctuate greatly on a monthly basis throughout the study (Fig. 15). Relative biomass ranged from 9% in August to 30% in June. Mean biomass ranged from 13% at Eldorado Canyon to 19% at Katherine's Landing. The most important species in the >11<21 um size fraction were Glenodinium pulvisculus, Cryptomonas marssonii, and Stephanodiscus astraea var. minutula.

The >44<64 um size fraction was of minor importance to overall annual phytoplankton biomass, contributing only 6 percent of the biomass. Large seasonal fluctuations were absent; relative biomass ranged from 3% in April to 9% in October and November. Mean annual biomass ranged from 3% at Eldorado Canyon to 11% at Katherine's Landing. The most abundant species in this fraction were Oocystis gigas var. incrassata, Cryptomonas rostrotiformis, and Dinobryon divergens.

Lake Havasu

The >21<44 um size fraction was also the main component of the Lake Havasu phytoplankton community, contributing 37% of the phytoplankton biomass (Table 20).

Netplankton contributed 23 percent to total biomass and phytoplankton >11<21 um were the third most abundant biomass component in Lake Havasu. Collectively, biomass <20 um accounted for 30% of the annual lake biomass. The other size fractions were of minor importance

to lake biomass.

The annual mean biomass of the size fraction >21<44 um was similar at all stations in Lake Havasu (Table 17). Seasonally, Havasu City showed high spring relative biomass (61%), while winter composition ranged from 3% in Upper Lake Havasu to 46% in Havasu City and 70% near Parker Dam (Table 17). On a monthly basis, biomass of >21<44 um phytoplankton did not fluctuate greatly, ranging from 29% in June to 57% in March (Fig. 16). The main taxonomic components of this size fraction were Cryptomonas erosa, Peridinium elpatiewskyi, and Anomoeoneis vitrea (Table 19).

Biomass of cells >64 um was highest at Upper Lake Havsau and lower down-lake at Havasu City and Parker Dam. Seasonally, high biomass in this fraction occurred during spring (42%) and fall (53%) in Upper Lake Havasu. Monthly mean biomass of the >64 um size fraction ranged from 8% in June to a maximum in October of 41% of total biomass. Two peaks were evident, occurring in May and October (Fig. 16). The dominant species during these months were Ceratium hirundinella fa. piburgense (May) and, Synedra ulna (October) in Upper Lake Havasu and the cyanophyte, Raphidiopsis curvata was dominant in May and October at Havasu City and Parker Dam.

Phytoplankton biomass <20 um accounted for 38 percent of the annual lake biomass. Phytoplankton >11<21 um was the main component, contributing 17%. The <5 um fraction ranged in biomass from 3% during September to 13% in November. No large monthly biomass fluctuations were apparent (Fig. 16).

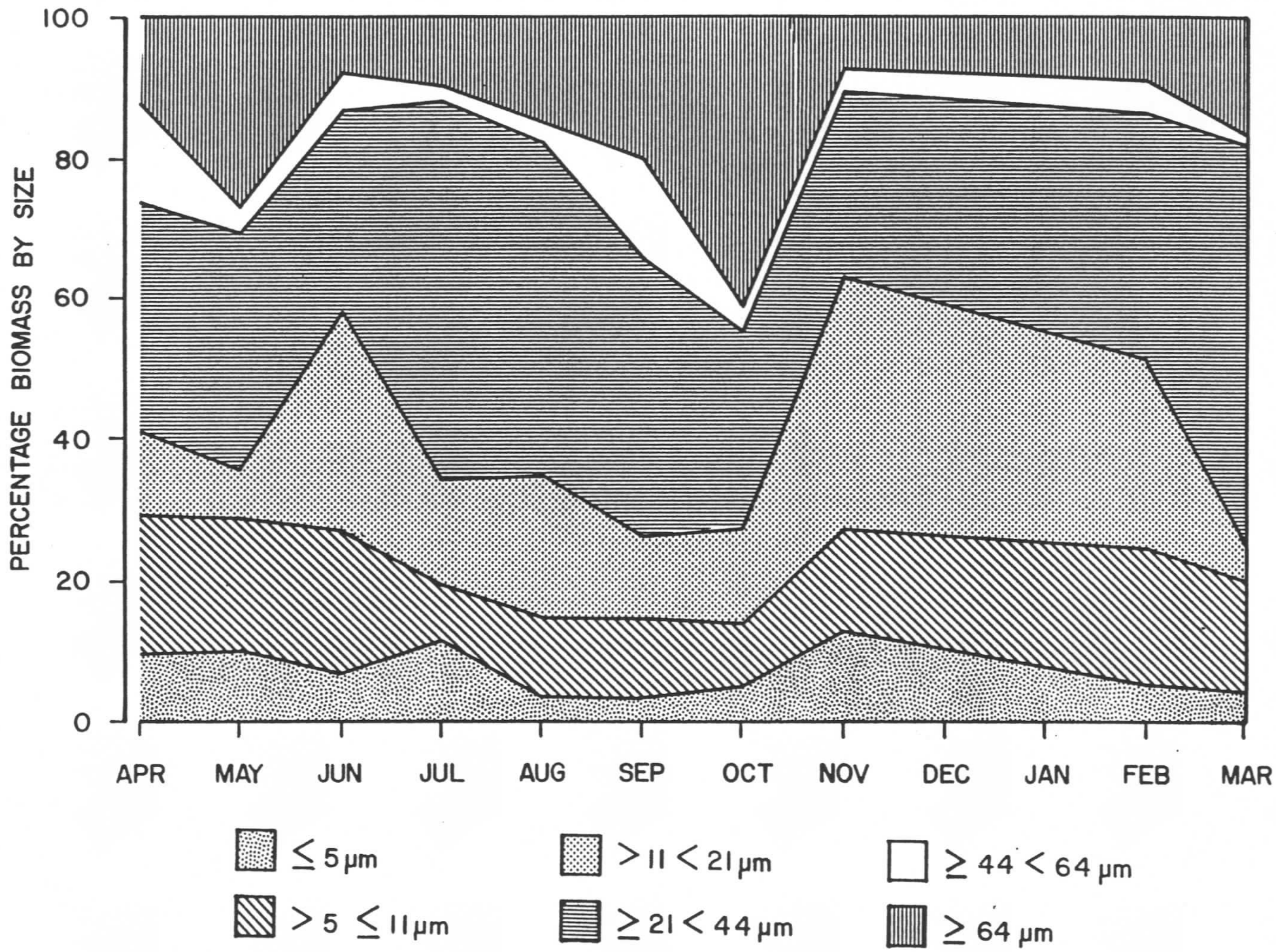

Figure 16. Monthly percentage phytoplankton biomass by size in Lake Havasu.

Biomass in the >5<11 um fraction ranged from 8% in July to 20% in June, with no large seasonal fluctuations. The most common species were *Rhodomonas minuta*, *Pseudopedinella erkensis*, and several unidentified flagellates. The >5<11 um size fraction was high in spring and winter at Havasu City and Upper Lake Havasu. Annual mean biomass was similar at all stations sampled.

Biomass in the >11<21 um fraction was highest at Parker Dam where relative biomass was 22% of the total. On a monthly basis, values ranged from 5% of total biomass in March to high of 36% in November and 27% in January. The peak in June occurred when *Cryptomonas marssonii* and *Dinobryon divergens* were most abundant. The most common species in the >11<21 um size class were *Glenodinium armatum*, *Cryptomonas marssonii*, and *Cyclotella meneghiniana* (Table 19).

Distribution of Phytoplankton Volumes

Phytoplankton biomass distribution in Lake Powell based on the mean equivalent spherical diameter (ESD) of the 38 of the most abundant species are presented in Fig. 17. Equivalent spherical diameter is the diameter of a sphere of equivalent volume (um^3) to the mean volume of a particular phytoplankton species. Fig. 17 represents 90 percent of total annual Lake Powell biomass. This figure shows the size structure of community biomass based on a continuum from 2 to 64 um. Distribution of phytoplankton particles is skewed towards the larger-sized cells with 44 percent of total biomass contributed by cells larger than 32 um ESD. The biomass peak near 32 um is due to the abundance of *Synedra ulna* (ESD 35 um) and *Fragilaria crotonensis* (ESD 34 um). Biomass peaks

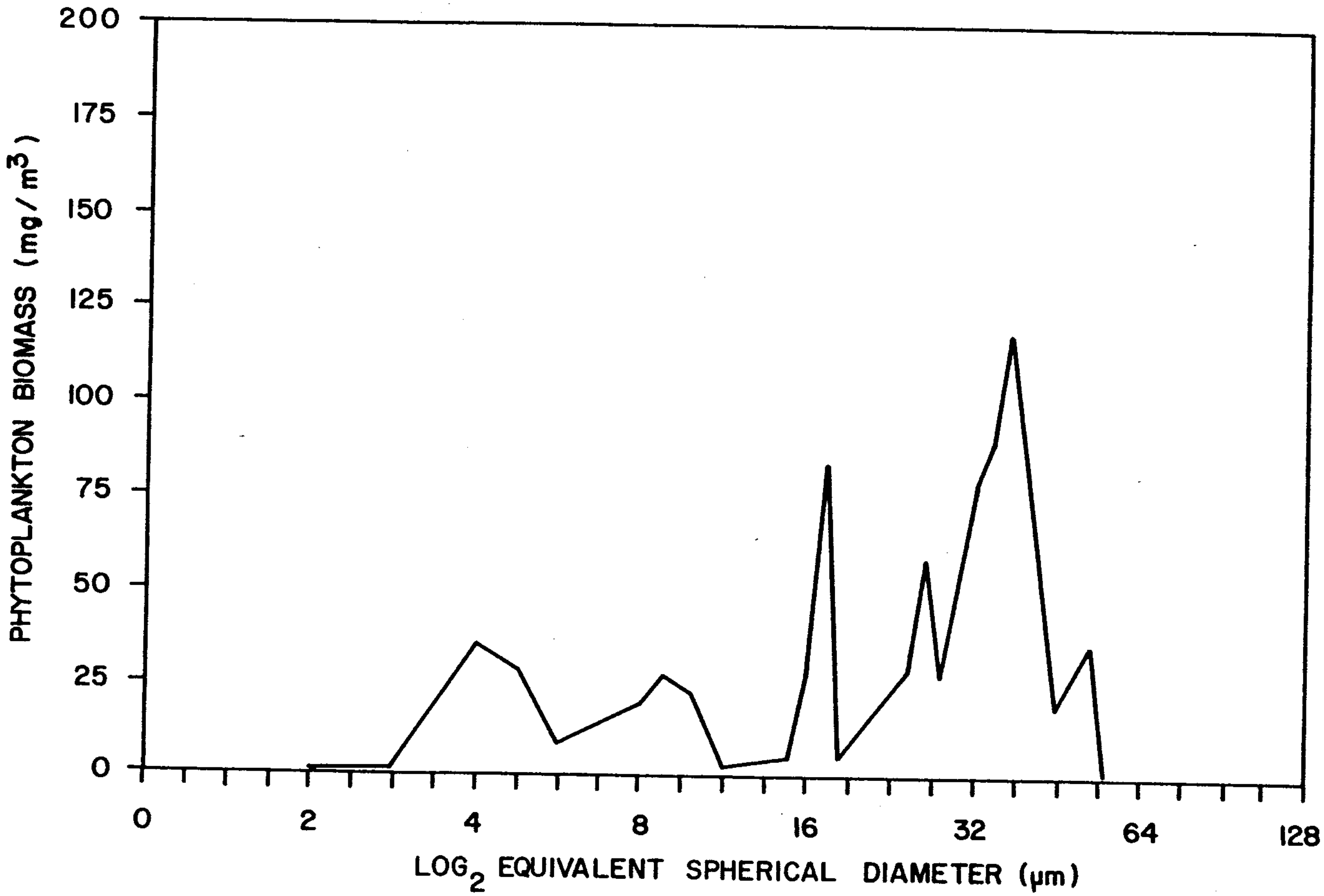

Figure 17. Equivalent spherical diameter of phytoplankton biomass in Lake Powell.

are also evident at 16 um and 4 um ESD. *Cryptomonas erosa* with an ESD of 16.5 um and *Rhodomonas minuta* and *Chrysochromulina parva* with, ESD's of 5.6 and 3.6 um, respectively, were main components of these peaks. Only 13 percent of total phytoplankton biomass occurred in cells less than 8 um ESD.

The size class distribution of biomass in Lake Mead, based on equivalent spherical diameter, is presented in Fig. 18. This figure represents 90 percent of total Lake Mead biomass based on mean biomass and ESD of the 30 most abundant species. Mean ESD values ranged from 2 um for small flagellates to 74 um for *Lyngbya birgei* filaments. Fifty-seven percent of total biomass was greater than 16 um ESD and 30 percent was less than 8 um ESD. Two biomass peaks were apparent, at 8 and 32 um ESD. The species largely responsible for these peaks were *Anomoeoneis vitrea* (ESD 8 um) and *Synedra ulna* (ESD 35 um).

Mean ESD biomass of 52 most abundant species which contributed 80 percent of total Lake Mohave biomass is presented in Fig. 19. Three biomass peaks based on ESD were present with 99 percent of the total in cells less than or equal to 32 um ESD and 40 percent of the total present in cells less than or equal to 8 um ESD. The dominant species in these peaks were *Rhodomonas minuta* (ESD 5 um), *Raphidiopsis curvata* (ESD 7.5 um) and *Anomoeoneis vitrea* (ESD 7.8 um), and *Peridinium cunningtonii* (ESD 26.8 um).

Size-class distribution of biomass based on ESD in Lake Havasu is presented in Fig. 20. This figure represents 86 percent of the total annual biomass in Lake Havasu and is based on the biomass and mean ESD of fifty species. The main biomass peak occurred near 8 um

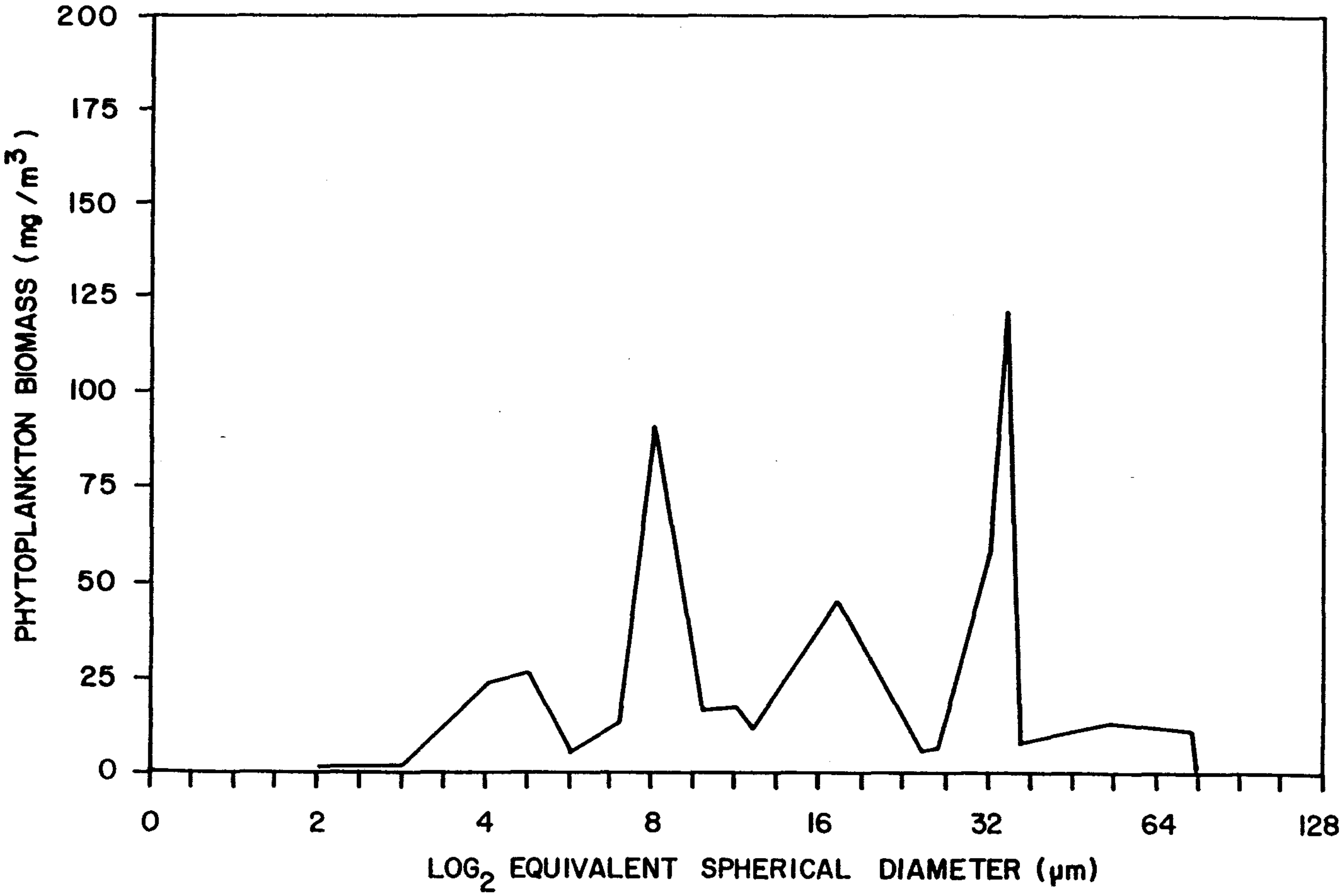

Figure 18. Equivalent spherical diameter of phytoplankton biomass in Lake Mead.

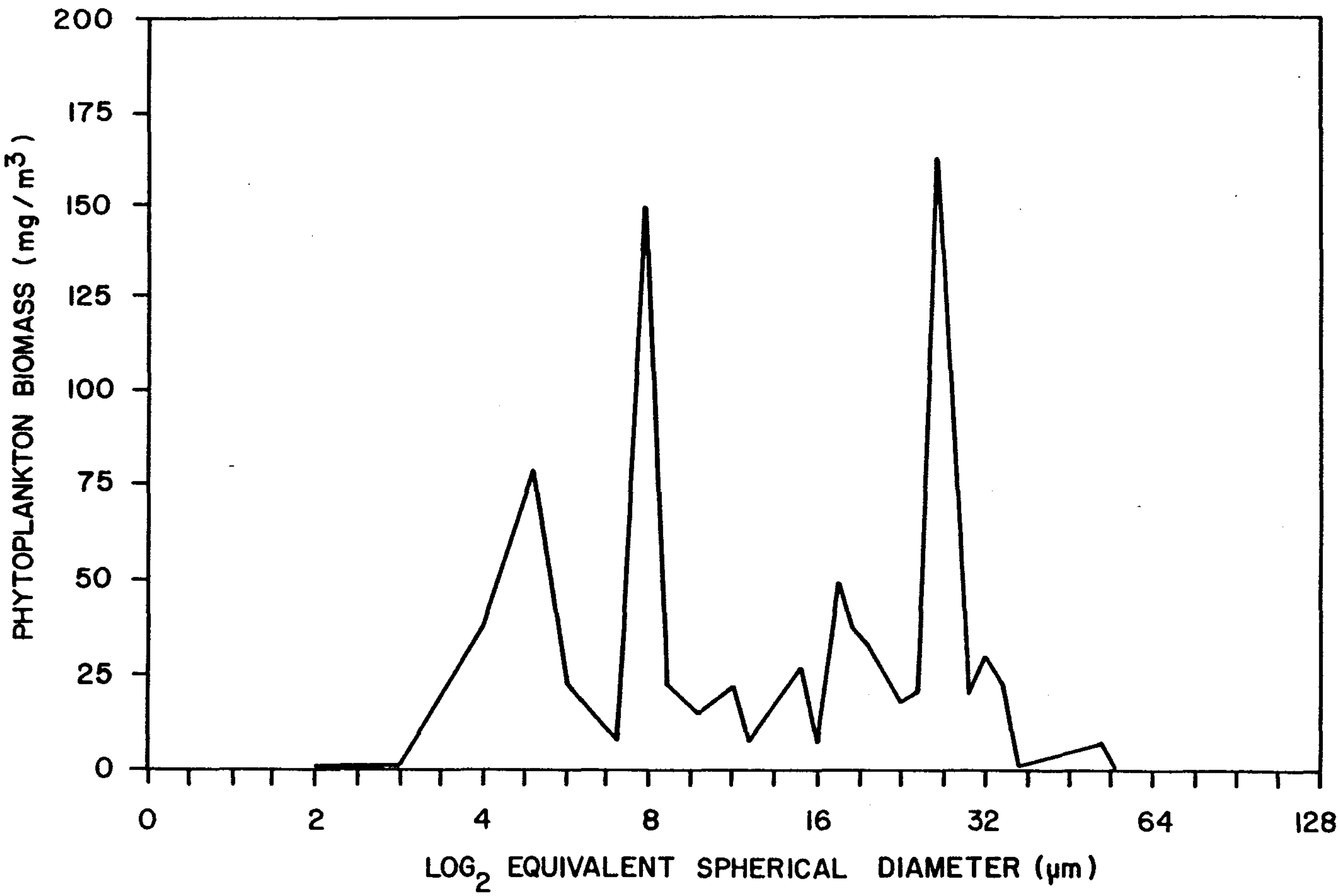

Figure 19. Equivalent spherical diameter of phytoplankton biomass in Lake Mohave.

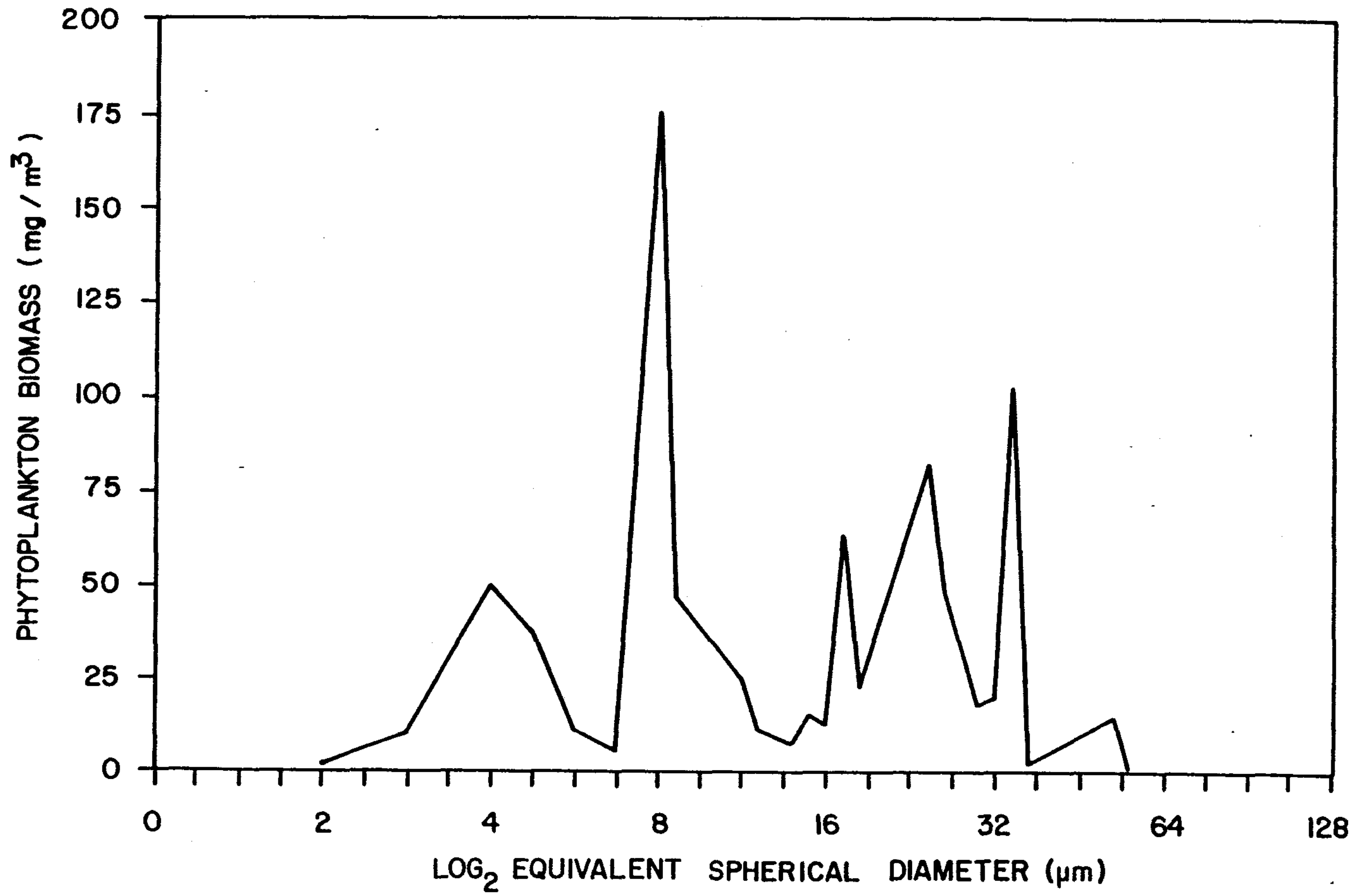

Figure 20. Equivalent spherical diameter of phytoplankton biomass in Lake Havasu.

Species most abundant in the-class ESD size interval around 8 um

Anomoeoneis vitrea, and Raphidiopsis curvata. Highest biomass

ed in the 4-8 um and 16-32 um ESD intervals. Fifty percent of the

biomass was present in the ESD interval less than or equal to 16

DISCUSSON

Species occurrence in each reservoir is presented in Appendix A. This species list, although the most complete one presently available, likely could be expanded with more frequent sampling and greater attention to diatom taxonomy. Also, phytoplankton sampling at one-month intervals is too infrequent to accurately describe the population dynamics of cells with potential cell division rates of one day.

The percentage occurrence of some common species in each reservoir is given in Table 12. *Cyclotella bodanica* var. *michiganensis* was present in more than one third of Lake Powell samples, only 13% of Lake Mead's, and was not observed in the lower reservoirs. *Cyclotella michiganiana* was present in over 50% of the Lake Powell and Lake Mead samples, but was absent or was observed in few samples in lakes Mohave and Havasu. *Raphidiopsis curvata* was present in more than 40% of lake's Havasu and Mohave samples but was found only occassionaly in lakes Powell and Mead. Other noteworthy species distributions were the absence of the two desmid species, *Cosmarium candianum* f. *minutum* and *Closterium aciculare* var. *subpronum* from Lake Mead. In Lake Powell,the non-occurrence of *Lyngbya birgei* and *Melosira varians* is of interest. *Chrysolykos planktonicus* Mack, a rare species, characteristic of cold-stenothermic, oligotrophic conditions (Pavoni 1963, Munawar and Munawar 1978), was found in Lake Havasu. *Dinobryon divergens* was found

in 49-77% of the four reservoir samples. This species is known to grow at low phosphorus concentrations (Hutchinson 1967, Wetzel 1983). The presence of Rhodomonas minuta in every sample and Chrysochromulina parva in more than 98%, demonstrates the eurytopic nature of these small flagellates (Table 12).

The factors regulating a eurytopic species such as R. minuta are not well known. Recent investigations have shown that competition for nutrients is the principal factor in determining species composition (Fuhs et al. 1972, Knoechel and Kalff 1978, Tilman 1977). This composition is further modified by differential effects of light and temperature on growth rates (Morgan and Kalff 1979). In cells coexisting under conditions of P-limitation, nutrient (phosphorus) uptake rates are strongly correlated with size (Smith and Kalff 1982).

Among the four reservoirs studied, total phytoplankton biomass, based on areal weighted means, was highest in Lake Havasu where values were 0.88 g/m^3 (Table 21). Lakes Powell and Mohave were similar with biomass of 0.78 g/m^3. Biomass concentrations in Lake Mead were less than one-half of the values measured in each of the other reservoirs.

Vollenweider (1968) suggested that maximum phytoplankton biomass might serve as an indicator of lake trophic status. He classified lakes as mesotrophic if mamimum annual phytoplankton biomass was 3-5 g/m^3 and ultraoligotrophic if biomass was 1 g/m^3. Munawar and Munawar (1982) proposed a classification based on mean phytoplankton biomass (Table 22). Their classification placed lakes with mean phytoplankton biomass of 1-2 g/m^3 in the mesotrophic category, while biomass less

Table 21. Reservoir and station trophic status based on maximum phytoplankton biomass (Vollenweider 1968), mean annual biomass (Munawar et al. 1982), and mean annual percentage biomass of size classes (um) ranked in order of abundance from highest (1) to lowest (6) in Lakes Powell (P), Mead (M), Mohave (V), and Havasu (H).

	Phytoplankton Biomass (g/m3)		Rank by Size Classes (um)					
	Areal weighted Mean	Mean	>64	>44<64	>21<44	>11<21	>5<11	<5
RESERVOIR					OLIGOTROPHIC			
V Lake Mohave	0.78	0.97	2	5	1	3	4	6
H Lake Havasu	0.88	0.93	2	6	1	3	4	5
P Lake Powell	0.78	0.84	1	3	2	5	4	6
M Lake Mead	0.34	0.52	1	5	2	3	4	6
	Range	Mean	>64	>44<64	>21<44	>11<21	>5<11	<5
STATION					MESOTROPHIC			
P Zahn Bay	0.18-5.6	1.97	1*	3	2	5	4	6
H Upper Lake Havasu	0.02-5.4	1.58	1	5	2	3	4	6
V Eldorado Canyon	0.09-4.5	1.54	4	6	1*	3	2	5
M Middle Las Vegas Bay	0.11-3.4	1.12	1*	6	2	3	4	5
Mean of ranks			1.8	5.0	1.8	3.5	4.0	5.5

(continued)

Table 21. (Continued)

		Range	Mean	>64	>44<64	>21<44	>11<21	>5<11	<5
					OLIGOTROPHIC				
P	Hite	0.13-2.7	0.96	2	4	1	3	5	6
H	Havasu City	0.01-1.7	0.74	3	6	1*	2	4	5
V	Cottonwood Basin	0.02-1.5	0.72	2	5	1	4	3	6
H	Parker Dam	0.02-2.0	0.70	4	6	1*	2	3	5
P	Wahweap Bay	0.15-2.2	0.63	1*	4	2	5	3	6
P	Hall's Crossing	0.22-1.0	0.61	2	3	1*	6	4	5
V	Katherine's Landing	0.01-2.2	0.58	3	5	1	2	4	6
	Mean of ranks			2.4	4.7	1.1	3.3	3.7	5.6
					ULTRA-OLIGOTROPHIC				
P	Oak Canyon	0.10-0.8	0.46	2	4	1*	5	3	6
M	Gregg Basin	0.01-1.1	0.33	1*	6	2	4	3	5
M	Boulder Basin	0.07-0.8	0.29	1	4	2	5	3	6
M	Virgin Basin	0.01-1.4+	0.28	1*	6	2	4	3	5
	Mean of ranks			1.3	5.0	1.8	4.5	2.8	5.5

* greater than 40% of annual biomass
+ classified as oligotrophic based on maximum biomass

Table 22. Lake trophic status classification scheme based on maximum phytoplankton biomass (Vollenweider 1968) and mean annual biomass (Munawar et al. 1982).

Trophic status	Phytoplankton biomass (g/m^3)	
	Mean	Maximum
Ultraoligotrophic	<0.5	1
Oligotrophic	>0.5-1.0	
Mesotrophic	>1.0-2.0	3-5
Mesoeutrophic	>2.0-4.0	
Eutrophic	>4.0-8.0	
Highly eutrophic	>8.0	>10

than 1 g/m^3 described oligotrophic lakes. These classifications are supported by the classification of Vollenweider et al. (1974) based on yearly primary production, chlorophyll a, and phosphorus loading.

According to these phytoplankton biomass-based classification schemes, lakes Powell, Mead, Mohave, and Havasu are all classified as oligotrophic waters (Table 20). Individual stations or basins within these reservoirs would be classified from ultra-oligotrophic to mesotrophic with mean total biomass ranging from 0.3 g/m^3 in Virgin, Boulder, and Gregg Basins of Lake Mead to 2.0 g/m^3 at Zahn Bay in the San Juan Arm of Lake Powell (Table 21). The stations with highest biomass, Zahn Bay, Hite, Middle Las Vegas Bay, Eldorado Canyon, and Upper Lake Havasu are close to nutrient-rich river inflows.

Inflows to lakes Powell, Mead, Mohave, and Havasu supply almost all of the nutrients, in contrast to most lakes which are fed from more diffuse inputs from the surrounding watershed. Reservoirs in a series such as lakes Powell, Mead, Mohave, and Havasu influence and are influenced by the other reservoirs in the series.

Seasonal timing of the major inflows to an impoundment affects stratification and formation of density currents. Density currents develop in lakes and reservoirs when entering and receiving waters are of different density. Temperature, and dissolved and suspended solids most commonly create density currents (Wunderlich and Elder 1973). Overflows (surface) form when the inflow is warmer or lower in TDS than the reservoir; underflows form when the inflow is colder or higher in TDS than the receiving waters. Interflows (midwater) develop where inflowing and receiving waters are at equal density.

Lakes Powell, Mead, Mohave, and Havasu are unique with respect to the flow characteristics and each affects the downstream impoundment differently. Spring inflows into Lake Powell carry large quantities of silt, are low in TDS, and are warm (17-20 °C). This warm, low salinity, and high sediment-bound phosphorus inflow enters Lake Powell as an overflow which may travel the entire length of the reservoir (Merritt and Johnson 1977). Phytoplankton biomass at Hite was higher than the down-lake stations in Lake Powell during the peak inflows. Nutrient uptake by phytoplankton may have reduced the availablity of nutrients to the down-lake stations, resulting in lower phytoplankton biomass.

Late summer and early fall inflows are lower in volume and suspended sediment, but are relatively higher in TDS than the spring-early summer overflow. This influent water has a slightly greater density than the lake water due to higher salinity, and forms an interflow which travels downstream at intermediate depths.

Late fall and early winter inflows are very cold (less than 10 °C), and less saline than earlier inflows. This inflow, greater in density than lake water, enters the lake as an underflow which travels the entire length of the lake from December to March. As a result this flow displaces bottom lake water and prevents anoxic conditions in the hypolimnion (Merritt and Johnson 1977).

Total inorganic phosphorus loading to Lake Powell in 1981 was 40 metric tons/yr with the Colorado and San Juan Rivers providing 70 and 30% of the total, respectively.

Thermal stratification in Lake Powell, persisting through

September, is induced as early as March by the overflowing density current coupled with surface solar heating (Gloss et al. 1980). Lake Powell is classified as warm, monomictic; the upper region of the lake is holomictic, while the lower, deeper area is meromictic (Merritt and Johnson 1977).

Density currents in Lake Mead were first described by Anderson and Prichard (1951). The depth and extent of the density current created by the Colorado River varied seasonally in relation to temperature. During winter (January-March), the cold river-water flowed along the bottom of the old river channel (thalweg). This underflow developed throughout the Upper Basin and occasionally reached Boulder Basin. During spring, the river-inflow was slightly cooler than lake-water and an underflow developed in Iceberg Canyon. Mixing with lake water increased the inflow temperature and an overflow was formed in Gregg Basin. With decreased flow from the Colorado River and increased salinity during the summer, an interflow was created. Reduced fall river temperatures created an underflow that developed in Gregg Basin and moved down-lake to Temple Bar and Virgin Basin (Paulson et al. 1980).

Las Vegas Wash is an important source of nutrients for for Lake Mead, providing 60% of inorganic phosphorus loading in 1981. Of the 152 metric tons of inorganic-P loading to Lake Mead in 1981, Las Vegas Wash and the Colorado River contributed 87 and 59 metric tons, respectively. The Muddy and Virgin Rivers contributed 6 metric tons of inorganic-P in 1981.

The extremely low phytoplankton biomass in the Upper Basin of Lake Mead appears to be caused by phosphorus-deficient conditions resulting

from reduced input of suspended sediment-bound phosphorus through Glen Canyon Dam (Paulson and Baker 1981). High phytoplankton biomass at Middle Las Vegas Bay appears to be a response to phosphorus loading from Las Vegas Wash.

Lake Mohave is supplied by nutrients from the hypolimnetic discharge from Hoover Dam which is located at a depth of 83 m (at an operating level of 364 m) and is characterized by high dissolved nitrogen and phosphorus. Inorganic-P loading to Lake Mohave in 1981 was 70 metric tons. Phytoplankton biomass below Hoover Dam at Eldorado Canyon was higher than biomass in the down-lake stations as a result of the greater nutrient supply. Discharge from Hoover Dam into Lake Mohave forms an underflow during most of the year due to the cold (12-13 °C), denser water. During the winter months, the Colorado River and Lake Mohave were at nearly equal temperatures. Complete mixing was apparent in up-lake areas during the winter. During periods of high discharge a cold-water wedge was formed in up-lake areas. The fluctuating high and low discharge of cold water created much instability in the temperature structure and circulation in the upper end of Lake Mohave (Paulson et al. 1980). The location of the interface of cold, nutrient rich water and warmer lake water during the summer strongly increases primary productivity at the interface (Priscu et al. 1982).

Temperature and circulation patterns in Lake Havasu are least studied and understood of the four mainstem reservoirs. Lake Havasu is fed by the relatively nutrient rich water from the hypolimnetic discharge from Davis Dam. Inorganic-P loading to Lake Havasu was 40 metric tons in 1981. The shallow depth of Lake Havasu and relatively

cold discharge from Davis Dam causes extensive mixing to occur throughout the year. Phytoplankton biomass was highest at Upper Lake Havasu throughout the study as a result of increased nutrient supplies.

Total phytoplankton biomass in lakes Powell, Mead, Mohave, and Havasu appears to be set by nutrient (phosphorus) concentration and availability. Positive relationships between nutrient concentration and phytoplankton biomass are well documented (Jones and Bachmann 1976, Kalff and Knoechel 1978, Schindler 1978). However, the factors determining size partitioning of phytoplankton biomass within the total component are less understood.

The three main forces regulating phytoplankton biomass size structure appear to be interspecific nutrient competition, selective predation, and reservoir morphometry and retention time. Pavoni (1963) was one of the first to investigate the relationship between nannoplankton and lake trophic or nutrient status. She stated that the contribution of nannoplankton to the productivity of lakes may be more important in oligotrophic than eutrophic systems, since, in the latter, nannoplankton volume may be markedly reduced due to high netplankton biomass. Watson and Kalff's (1981) work supported the hypotheses that with increasing eutrophication (i) nannoplankton biomass increases and (ii) if trophic status is defined by total algal biomass, the relative proportion of nannoplankton biomass decreases. However, Munawar and Munawar (1975) reported high relative percentages of nannoplankton in ultraoligotrophic Lake Superior as well as in eutrophic Lake Erie. Their studies on the Laurentian Great Lakes have shown that nannoplankton possess characteristic and flexible nutrient kinetics

adapted to varying light, temperature and nutrient conditions ranging from pristine environment to eutrophic waters.

Nannoplankton (when defined as cells <64 um) contributed as much as 58% of biomass in Lake Mead and 85% in Lake Mohave (Table 20). In lakes Powell and Mead, the size fraction >64 um was the main biomass component in contrast with the down-lake reservoirs, Mohave and Havasu, where >21<44 um fraction was most abundant (Tables 20, 21). In three of the four stations classified as mesotrophic, Zahn Bay (Lake Powell), Upper Lake Havasu, and Middle Las Vegas Bay (Lake Mead), netplankton was the dominant size fraction. However, in two of the four stations, Gregg and Virgin Basins (Lake Mead), classified as ultraoligotrophic, based on mean annual biomass, netplankton contributed greater than 40 percent of annual phytoplankton biomass and was first in Middle Las Vegas Bay (Tables 14, 20, 21).

Watson and Kalff (1981) computed regression equations to predict nannoplankton biomass based on total phytoplankton biomass. Prediction of nannoplankton biomass in this study based on Watson and Kalff's work is difficult because of different phytoplankton sizes used to define nannoplankton. Watson and Kalff used 30 um and I used 64 um as the separation between nannoplankton and netplankton. I calculated the predicted nannoplankton biomass based on Watson and Kalff's work and found close agreement of the predicted and observed values only in 1 of the 4 reservoirs (Lake Powell) when nannoplankton were defined as cells <44 um.

Nannoplankton biomass predicted by Watson and Kalff's equations and the observed nannoplankton (<44 um) percentage biomass are presented in

Table 23. Predicted and observed percentage nannoplankton biomass based on Watson and Kalff's (1981) regression equation*.

Reservoir	Predicted (%)	Observed (%)
Lake Powell	47	54
Lake Mead	69	53
Lake Mohave	47	79
Lake Havasu	44	72

* Log (nanoplankton biomass) = 0.53 log (total biomass) + 1.03

Table 23.

Non-parametric statistical testing using Kruskall-Wallis showed no significant differences ($p < 0.05$) among individual size classes and station trophic status. However, when ranked station percentage biomass size class data are grouped by reservoir, instead of trophic status, significant differences ($p < 0.1$-0.05), were found among reservoirs for four of the six size classes. Based on the findings of previous studies (Pavoni 1963, Watson and Kalff 1981), I would have expected lakes Mohave and Havasu to support a smaller percentage of nannoplankton than the more unproductive locations, especially the upper Basin of Lake Mead.

Uptake of phosphorus and nitrogen, as a function of nutrient concentration, follows Michaelis-Menton kinetics (Tilman and Kilham 1976, Dugdale 1967). Maximium uptake velocity (V_{max}) and half-saturation constants for uptake (K_s) are species, group, or size specific (Malone 1980). However, quantification of uptake rates alone does not provide enough information to characterize the utilization of nutrients by a species (Kilham 1978). The effeciency of conversion of a resource into offspring is more important tham how fast an organism eats. Thus, growth kinetics rather than nutrient kinetics are needed in formulating competition models (Kilham and Kilham 1980).

If competition for resources were the primary selection pressure, all phytoplankton cells would be expected to be small, and small cells with low K_s values should predominate in oligotrophic waters. Smaller phytoplankton cells are generally more successful in competition for nutrients than larger cells (Laws 1975, Schlesinger et al. 1981). In nutrient poor waters, competition may contribute to greater abundance

and growth rates of small phytoplankton relative to large size phytoplankton (McCarthy et al. 1974, Watson and Kalff 1981).

Nannoplankton, with high rates of decomposition (Pavoni 1963), may also have greater influence on nutrient cycling in deep (lakes Powell and Mead) and oligotrophic lakes. Many of these species, including Rhodomonas minuta, lack cell walls and undergo lysis upon death (Taylor and Wetzel 1983). Nannoplankton may provide critical amounts of nutrients particularly at deeper depths (Munawar et al. 1978). Rigler (1973) suggested that phytoplankton <30 um and bacteria take up phosphate and exchange it more rapidly with the PO_4-P pool in the medium. Phytoplankton >30 um often comprise a larger particulate phosphorus pool through which phosphorus cycles more slowly. Work by Burnison (1975) and Paerl and Lean (1976) support these observations.

Nannoplankton, and particularly phytoflagellates, may be better able to exploit nutrient patches than larger, non-motile forms. Since a cell's surface area defines the area across which nutrients can pass, high surface-to-volume should allow maximum rates of nutrient uptake, photosynthesis, and growth (Malone 1980). Movement through the water may renew the supply of inorganic molecules existing at low concentration (Hutchinson 1967). Phytoflagellates also may better utilize the miniature patches of dissolved phosphate produced by individual zooplankton (Lehman and Scavia 1982).

Based on trophic status and nutrient concentrations, nannoplankton would be expected to dominate in these reservoirs. This is true in lakes Mohave and Havasu, however, netplankton dominance in the upper reservoirs may be due to factors other than nutrient concentration. The

phytoplankton size structure in Lake Mead appears paradoxical based on nutrient concentrations. Paulson and Baker 1981) reported that the Upper Basin of Lake Mead is severely phosphorus-deficient, however, the phytoplankton community in Lake Mead is dominated by cells >64 um (Table 14). Guillard and Kilham (1977) reported similar results in oceanic regions where small-sized diatoms predominated in nutrient rich waters and large-celled species were characteristic of nutrient-poor waters. Kilham and Kilham (1980) suggested an evolutionary explaination for this apparent paradox. The argument for evolutionary ecology is that in stable, nutrient-poor environments, large cells may be favored which delegate a higher proportion of their metabolic resources to processes other than rapid growth rates. A lower rate of offspring production, but more efficient use of resources to maximize metabolic efficiency would increase the chances of offspring surviving to reproduce. Freshwater environments are more environmentally unstable than open ocean systems. However, on a scale of relative stability, lakes Mohave and Havasu would be considered less stable than lakes Powell and Mead due to the shallow depth and short retention time in Mohave and Havasu.

Morphometry of lakes Powell and Mead is different from the down-lake reservoirs, Lake Mohave and Lake Havasu. Powell and Mead have much greater surface areas and volume. These two reservoirs also have irregular shorelines (shoreline development of 26.0 and 9.7 for Powell and Mead, respectively, compared to <3.0 for Mohave and Havasu). Mead and Powell have much greater maximum and mean depths, and hydraulic retention times are 3-4 years compared to <0.2 years in Mohave and Havasu.

Since nannoplankton have lower sinking and higher decomposition and reproductive rates than netplankton (Pavoni 1963, Munawar et al. 1978), they have a much greater influence on metabolic exchange in the epilimnion and metalimnion, particularly in deeper lakes.

Size selective predation may greatly affect size distribution of phytoplankton biomass. Numerous studies have reported on the interrelationships of nannoplankton and zooplankton. Grazing pressure of zooplankton on nannoplankton would be expected to be greater in lakes with a high percentage or production of nannoplankton, than in lakes with a lower percentage such as eutrophic lakes (Kristiansen 1971). Porter's (1973) selective grazing experiments revealed that the major effect of grazing was the suppresson of small algae, primarily flagellates and nannoplankton. Gliwicz (1975) observed that density changes of filter-feeding zooplankton and thus, changes in grazing pressure, may have a significant impact on species and size structure of phytoplankton. Gilbert and Bogdan (1981) reported that rotifers, Keratella and Polyarthra preferred flagellated algal cells. Nannoplankton, which are present in higher proportions in Lake Mohave and Lake Havasu, may be less sensitive to grazing pressure than in Lake Mead and Lake Powell.

In summary, the results of this study have shown that lakes Powell, Mead, Mohave, and Havasu are, on a lake-wide scale, unproductive waters. River inflows create spatial heterogeneity in nutrients, temperatures, and phytoplankton biomass and size structure. Reservoir morphometry and retention time are also important in determining the phytoplankton community. Short retention time, shallow depth and

thermal instability in lakes Mohave and Havasu appear to promote the abundance of nannoplankton. However, the factors combining to regulate reservoir or natural lake phytoplankton are extremely complex. Sampling intervals should be timed at intervals closer to the reproductive interval of the species in question. Most nannoplankton species have turnover times of a day, however, many of these common species are difficult to maintain in culture, and information on growth rates are limited (Klaveness 1981).

Knowledge of the proximate (mechanistic) and ultimate (evolutionary) influences on phytoplankton size-structure may help in understanding these and other puzzling questions in phytoplankton ecology.

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Appendix A. Species composition, cell volume, size class, and occurence in Lake Powell (P), Lake Mead (M), Lake Mohave (V), and Lake Havasu (H) during February 1981 to March 1982. Cell volumes are for individual cells unless denoted by (*). Size class categories are based on longest mean linear measurement. Size classes: 1 (<5 um), 2 (>5<11 um), 3 (>11<21 um), 4 (>21<44 um), 5 (>44<64 um), and 6 (>64 um).

Size class	Taxon	Cell volume (um3)	Location
	CHLOROPHYTA		
4	*Actinastrum hantzschii* Lagerheim.	35.997	P,V,H
3	*Akanthochloris* sp.	1022.650	M
4	*Ankyra judayi* G. M. Smith	92.220	P,M,V,H
5	*A. judayi*	209.440	M
6	*A. judayi*	224.493	M
4	*Ankistrodesmus* sp.	31.416	P,M,V
4	*A. falcatus* (Corda) Ralfs	159.043	M
3	*Aulacomonas submarina* Skuja	265.072	V
6	*Botryococcus braunii* Kuetzing	344.791	P,M,V
2	*Carteria* sp.	268.083	V,H
3	*Carteria* spp.	502.655	M
2	*Carteria globosa* ?	356.818	H
2	*Chlamydomonas sp.*	268.083	P,V,H
1	*C.* sp.(4-5 um)	33.510	P,M,V,H
2	*C.* sp.(6-8 um)	50.265	P,M,V,H
3	*C.* sp.	1129.010	P,V,H
2	*C. globosa* (Snow)	194.910	P,M,V,H
2	*C. gloephila* Skuja	13.195	P,M,V,H
3	*C. orbicularis* Pringsh.	230.907	P,M
2	*Chlorella* sp.	65.450	P,M,V,H
3	*Chlorogonium* sp.	104.720	H
3	*C. metamorphum* Skuja	88.750	H
2	*C. minimum* Playfair	47.124	V,H
6	*Closterium aciculare* var. *subpronum* W. and G. S. West	2896.730	P,V,H
6	*C. acutum* var. *variabile* Lemmermann) Kreiger	393.152	P,V,H
3	*Coelastrum cambricum* Archer	268.083	P

Appendix A. (Continued)

Size class	Taxon	Cell volume (um3)	Location
4	*C. cambricum*	113.097	M,V,H
4	*C. cambricum* var. *intermedium* (Bohlin) G. S. West	113.097	M
4	*C. microporum* Naegeli	523.599	P,M,V,H
4	*C. proboscideum* Bohlin	65.450	P,M,H
4	*C. reticulatum* (Daug.) Senn.	179.594	P,M
3	*Coelastrum reticulatum* var. polychordon Korchikov	179.594	M
3	*C. sphaericum* Naegeli	143.793	H
4	*C. sphaericum*	523.599	P,M,V,H
4	*Cosmarium* sp.	15315.300	P,M,V,H
4	*Cosmarium candianum* f. *minutum* Compere	9952.980	P,V,H
3	*Crucigenia rectangularis* (A. Braun) Gay	67.021	P,M,V,H
4	*C. rectangularis*	67.021	M
2	*C. tetrapedia* (Kirch.) West and West	75.000	H
3	*C. tetrapedia*	128.000	H
3	*Dictyosphaerium pulchellum* Wood	65.450	H
4	*D. pulchellum*	130.000	P,M,H
5	*D. pulchellum*	130.986	P,V,H
4	*Echiosphaerella limnetica* G. M. Smith	356.818	P,M,V,H
3	*Echinocoleum elegens* Jao and Lee	98.175	M
6	*Elakatothrix gelatinosa* Wille	54.192	P,M,V,H
4	*Eudorina elegans* Ehrenberg.	662.478	P,M,V
5	*E. elegans*	633.463	P,M,V,H
3	*Franceia droescheri* (Lemm.) G. M. Smith	118.791	P,M
3	*Furcilia* sp.	368.614	H
3	*Furcilia lobosa* var. *stigmatophora* Skuja	1227.180	V
3	*Gloeocystis* sp.	104.720	P,M,V,H
4	*Gloeocystis gigas* (Kuetz.) Lagerheim	4188.790	M
2	*Golenkinia paucispina* West and West	130.924	M
2	*G. radiata* (Chod.) Wille	362.195	P,M,V,H
3	*G. radiata*	1022.650	V
3	*Gyromitus* sp.	402.124	P,M
3	*Gyromitus cordiformis* Skuja	250.000	P
4	*Kirchneriella* sp.	28.274	P
4	*Kirchneriella contorta* (Schmidle) Bohlin	28.274	P
4	*K. lunaris* (Kirch.) Moebius	28.274	H
3	*Lagerheimia* sp.	900.000	M,V
3	*L. ciliata* (Lag.) Chodat	972.124	P,V,H

Appendix A. (Continued)

Size class	Taxon	Cell volume (um3)	Location
3	L. quadriseta (Lemm.) G. M. Smith	200.000	P,M
3	L. subsalsa Lemmermann	837.758	M,V,H
2	L. wratislawiensis (Schrader) Ley	23.500	H
3	L. wratislawiensis	23.562	M,V,H
2	Mesostigma sp.	400.000	P
4	Micractinium pusillum Fresenius	46.676	P,H
4	Monoraphidium setiforme (Nyg.) Kom.-Leg.	9.512	M,V,H
5	M. setiforme	14.464	P,V,H
6	M. setiforme	20.000	V
6	Mougeotia sp.	1530.350	P,M,V,H
2	Nephroselmis discoidea Skuja	98.175	H
3	Nephrocytium limneticum G. M. Smith	179.600	P,M,V,H
4	N. limneticum	180.000	M
6	Oedogonium sp.	1000.000	V
3	Oocystis sp.	67.021	M,V,H
4	O. borgei Snow	865.520	P,M,V,H
4	O. gigas var. incrassata W. and G. S. West	8504.430	P,M,V,H
5	O. gigas var. incrassata	8504.430	P,M,V,H
3	O. lacustris Chodat	1055.580	V
4	O. lacustris	3351.030	M,V,H
4	O. parva West and West	559.555	P,M,V,H
4	O. pusilla Hansgirg	127.235	P,M,V,H
3	O. submarina Lagerheim	858.316	P
3	Pandorina morum (Muell.) Bory	648.652	P,M,H
4	P. morum	641.431	P,M,V,H
5	P. morum	650.000	P,M,V,H
4	Pediastrum boryanum (Turp.) Meneghin.	*3534.290	P,M,V,H
5	P. boryanum	*12673.100	P,M,V,H
5	P. duplex Meyen	*6283.190	P,M,V,H
6	P. duplex var. clathratum (A. Braun) Lagerheim	*29044.000	V
3	P. integrum Naegeli	*4778.360	P
3	P. muticum Kuetzing.	*3019.070	P
3	P. muticum var. crenulatum Prescott	*3019.070	P
6	P. simplex (Meyen) Lemmermann	*3848.450	P,M,V
3	P. tetras (Ehrenberg.) Ralfs	*883.573	P
1	Pedinomonas minutissima Skuja	5.760	P,M,V,H
4	Planctonema lauterbornii Schmidle	30.434	P,M,V,H
5	P. lauterbornii	30.430	P,M,V,H
6	P. lauterbornii	30.434	P,M,V,H
4	Platydorina caudata Kofoid	407.720	M
3	Platymonas elliptica G. M. Smith	1048.690	P,M,V,H

Appendix A. (Continued)

Size class	Taxon	Cell volume (um3)	Location
2	Polyblepharides sp.	50.00	M
3	Polyblepharides sp.	82.467	V
2	Polytoma minus ? Pascher	79.522	P
3	Polytoma sp.	247.989	M,V
3	Polytoma granuliferum Lack.	628.319	P
3	Polytomella caeca Pringsh.	1150.350	V,H
4	Quadrigula chodatii G. M. Smith	105.747	P,M,V
5	Q. chodatii	100.531	P,M
4	Roya obtusa (Breeb) West and West	264.627	M,V
2	Scenedesmus sp.	24.544	P,M,V,H
3	S. abundans (Kirch.) Chodat	24.435	P,M,V,H
3	S. acuminatus (Lag.) Chodat	54.192	P,V
3	S. arcuatus Lemmermann	67.021	P,V
4	S. arcuatus var. platydiscus G. M. Smith	119.991	P,V,H
3	S. bicaudatus (Hansg.) Chodat	94.510	M,V
2	S. bijuga (Turp.) Lagerheim	62.622	P,H
3	S. bijuga	136.141	P,M,V,H
4	S. bijuga	316.000	P,M,V
3	S. bijuga var. alternans (Reinsch) Hansgrig	24.544	H
2	S. bijuga var. irregularis (Wille) G. M. Smith	24.544	P,M,H
2	S. denticulatus Lagerheim	32.725	V,H
3	S. dimorphus (Turp.) Kuetzing	129.918	P,M,V,H
4	S. dimorphus	603.186	P,M
3	S. dispar Breb.	51.836	V,H
3	S. ecornis (Ralfs) Chodat	58.643	P,M,V
4	S. ecornis var. disciformis Schod.	397.971	P,M,H
2	S. intermedius Chodat	11.584	P,M,H
3	S. obliquus (Turp.) Kutz.	47.124	P
3	S. opoliensis P. Richter	24.544	H
2	S. quadricauda (Turp.) de Brebisson	22.907	H
3	S. quadricauda	30.681	P,M,V,H
4	S. quadricauda	51.836	V
3	S. quadricauda var. longispina (Chodat) G. M. Smith	22.907	M
3	S. quadricauda var. longispina f. asymmerticus Hortob.	20.617	P
4	S. quadricauda var. maximus West and West	458.323	M,V,H
3	S. quadricauda var. quadrispina (Chodat) G. M. Smith	22.907	V
3	Scherffelia deformis Skuja	680.678	V
2	Selenastrum capricornutum Printz.	5.301	P,H

Appendix A. (Continued)

Size class	Taxon	Cell volume (um3)	Location
2	Selenastrum minutum (Naeg.) Collins	42.883	P,M,V,H
2	Sphaerocystis schroederi Chodat	212.414	P,M
3	S. schroeteri	212.000	H
4	S. schroeteri	212.000	P,M,V,H
5	S. schroederi	212.175	P,M,H
6	S. schroederi	213.036	H
5	Staurastrum sp.	10384.300	P,M,V,H
3	Tetraedron caudaum var. longispinum Lemmermann	54.000	H
2	T. minimum (A. Braun) Hansgrig.	126.150	P,M,V,H
3	T. minimum	250.000	H
3	T. minimum var. scrobiculatum Lagerheim.	250.000	M
1	T. muticum (A. Braun) Hansgrig.	30.800	P,M,V,H
2	T. muticum	53.768	P,M,V,H
3	T. pentaedricum West and West	100.000	H
3	T. trigonum	261.799	P
2	Tetrastrum staurogeniaeforme (Schroeder) Lemm.	*26.137	P,M,H
4	Treubaria setigerum (Archer) G. M. Smith	217.981	P,M,H
4	T. triappendiculata Bernard	143.793	M
	EUGLENOPHYTA		
4	Euglena sp.	335.103	P,H
5	E. sp.	3769.910	P,V,H
6	E. sp.	25955.800	H
4	Lepocinclis sp.	1966.390	M,H
4	Phacus sp.	4704.690	P,H
4	Phacus orbicularis var. zmudae Namyslowski	3909.540	P
2	Trachelomonas sp.	523.599	P
3	T. sp.	2904.690	P,H
4	T. sp.	1884.960	P
	PYRRHOPHYTA		
6	Ceratium hirundinella (Mueller) Schrank	88312.000	P,M,V,H
6	C. hirundinella fa. austriacum (Zederbauer) Bachmann	20257.000	P,H
6	C. hirundinella fa. brachioceroides Ostenfeld	20257.000	P,M,V,H
6	C. hirundinella f. furcoides	20256.800	P,M,V,H

Appendix A. (Continued)

Size class	Taxon	Cell volume (um3)	Location
	(Schroeder) Hub-Pest.		
6	*C. hirundinella* fa. *piburgense* Bachmann	82539.000	P,M,V,H
6	*C. hirundinella* fa. *robustum* (Amberg) Bachmann	88311.700	P,M,V,H
6	*C. hirundinella* fa. *scotticum* Bachmann	82539.000	P,M,V,H
6	*C. hirundinella* fa. *silesciacum*	50000.000	P,M,V,H
6	*Ceratium* (CYST)	10000.000	P,V,H
4	*Diplopsalis acuta* Entz.	18230.100	P,M,V,H
5	*D. acuta*	24374.300	P,M,V,H
3	*Glenodinium* sp.	1163.330	P,M,V,H
4	*G.* sp.	3909.540	P,V,H
4	*G. aceedans*	5539.680	H
4	*G. ambiguum* Thompson	7211.350	P,M,V,H
3	*G. armatum* Levander	2337.180	P,M,V,H
4	*G. gymnodinium* var. *biscutelliforme* Thompson	29751.900	P,M,V,H
3	*G. pulvisculus* Stein	3637.590	P,M,V,H
3	*Gymnodinium* sp.	466.526	P,M,V,H
4	*Gymnodinium* sp.	1227.180	M,V,H
3	*G. fungiaforme* Anissimowa	230.907	P,M,V,H
5	*G. helveticum* var. *achroum* Skuja	13441.300	P,M,V,H
2	*G. ordinatum* Skuja	477.359	P,M,V,H
5	*G. ubberimum* (Allman) Korfoid and Swezy	16591.500	P,V,H
4	*G. ubberimum* var. *rotundatum* ? (Klebs) Popovsky	3768.480	P,M,V,H
2	*G. varians* Maskell	259.181	V
3	*G. varians*	368.614	H
4	*Peridinium* sp.	5672.320	P,V,H
4	*P. bipes* var. *tabulatum* (Ehrenberg) LeFevre	19573.200	P,M,V,H
4	*P. cunningtonii* Lemm.	10037.800	P,M,V,H
4	*P. elpatiewskyi* (Ostenfeld) Lemm.	9193.610	P,M,V,H
3	*P. inconspicuum* Lemm.	2276.260	P,M,V,H
4	*P. quadridens* Stein	10233.900	P,M,V,H
5	*P. willei* Huitfeldt-Kass	61631.000	P
	CRYPTOPHYTA		
2	*Chroomonas* sp.	45.000	P,M,V
2	*Cryptaulax vulgaris* f. *rhomboidea* Nauwerck	117.810	P,M
3	*C. vulgaris* f. *rhomboidea*	148.080	P,M,V,H

Appendix A. (Continued)

Size class	Taxon	Cell volume (um3)	Location
2	Cryptomonas spp. (<11um)	174.227	V
3	C. sp.(11.1-20.9 um)	536.165	P,M,V,H
4	C. sp. (21-43.9 um)	3534.290	P,M,V
4	C. borealis Skuja	2789.680	V
3	C. brevis Schiller	1827.440	P
3	C. caudata Schiller	287.587	M,V
3	C. erosa Ehrenberg	1003.280	P,V,H
4	C. erosa	2340.600	P,M,V,H
3	C. erosa var. reflexa (S) Marsson	801.600	M
3	C. erosa var. reflexa	654.498	P,M,V
4	C. erosa var. reflexa	1130.000	P
3	C. marssonii Skuja	435.699	P,M,V,H
4	C. marssonii	820.601	P,V
3	C. ovata Ehrenberg	1028.320	P,V,H
4	C. ovata	2024.850	P,M,V,H
3	C. parapyrenoidifera Skuja	799.858	P
4	C. parapyrenoidifera Skuja	2035.230	P,H
3	C. pyrenoidifera Skuja	399.048	P,M,V,H
4	C. reflexa Skuja	1886.770	V,H
4	C. rostratiformis Skuja	4623.440	P,V,H
5	C. rostrotiformis	6870.790	P,M,V,H
4	C. tetrapyrenoidosa Skuja	1564.910	M
2	Katablepharis ovalis Skuja	91.011	P,M,V,H
3	K. notonectoides ? Skuja	163.625	M,V
3	Rhodomonas lens Pascher and Ruttner	381.376	P,M,V,H
2	R. minuta Skuja	79.796	P,M,V,H
3	R. minuta Skuja	127.010	M
2	R. minuta var. nannoplanctica Skuja	32.955	P,M,V,H
2	Sennia parvula Skuja	127.627	P,V,H
	CHRYSOPHYCEAE		
3	Bicoeca sp.	10.472	P,M,V
2	Bodo sp.	10.472	P,M,V,H
1	Chromulina sp.(<5um)	14.137	P,M,V,H
2	Chromulina sp.(6-8 um)	179.594	P,M,V,H
3	Chromulina sp.	402.124	H
2	Chrysamoeba sp.	91.952	P,M,V,H
2	Chrysamoeba microkonta Skuja	113.097	P,M,V,H
4	Chrysocapsa sp.	113.097	M
4	Chrysocapsa planktonika Pascher	87.114	M
1	Chrysochromulina parva Lackey	24.206	P,M,V,H
2	Chrysococcus sp.	220.893	P,M,V,H
3	C. heverlensis Conrad	654.498	P,M,V

Appendix A. (Continued)

Size class	Taxon	Cell volume (um3)	Location
2	C. radians Conrad	78.540	P,V,H
2	Chrysolykos planktonicus Mack	23.562	H
5	Dinobryon sp.	240.000	M
4	D. divergens Imhof	240.000	M,V,H
5	D. divergens	239.808	M,V,H
6	D. divergens	239.808	P,M
5	D. sociale	200.000	P
2	Erkenia subaequiciliata Skuja	50.265	M,H
3	Gloeoskene? turfosa	47.700	P,M,V,H
5	Codonosigopsis sp.	250.000	P
5	Codonosigopsis robinii Senn.	78.540	M,V,H
3	Heliochrysis eradians Pascher	65.450	V
3	Mallomonas sp.	654.498	P,M,V,H
3	M. acaroides Perty	1227.180	P,M,V,H
2	M. globosa Schiller	523.599	P,V
3	M. pseudocoronata Prescott	1433.160	V,H
4	M. pseudocoronata	2079.840	P,M,V,H
3	M. tonsurata var. alpina (Pascher and Ruttner)	663.672	P,M,V,H
1	Monochrysis parva Skuja	6.283	P,V,H
1	Ochromonas sp.	33.510	P,M,V,H
2	O. sp.	63.617	P,M,V,H
2	O. minuscula Conrad	78.976	P,M,V,H
2	O. sphagnalis Conrad	33.510	P,M,V,H
2	Parabodo sp.	42.412	P,M,V,H
2	Pseudokephryion sp.2	150.460	P,M,V,H
1	P. minutissimum Conrad	23.955	P,M,V,H
2	P. minutissimum	42.726	P,H
2	Pseudopedinella erkensis Skuja	204.079	P,M,V,H
3	Rhizochrysis sp.	696.910	M
4	Salpingoeca elegans (Bachmann) Lemm.	113.000	M
3	Sphaeroeca volvox Lauterborn.	78.540	H
	BACILLARIOPHYCEAE		
5	Auliscus caelatus f. tryptodiscus ? Bockm.	2500.000	P
3	Achnanthes lanceolata (Breb.) Grun.	198.540	V
3	A. minutissima Kuetzing.	94.755	P,M,V,H
2	Amphora perpusilla (Grun.) Grun.	233.097	V
6	Amphipleura pellucida Kuetzing.	5108.320	P,M
3	Anomoeoneis vitrea (Grun.) Ross	130.900	P,M
4	A. vitrea	244.609	P,M,V,H
6	Asterionella formosa Hass.	581.268	P,M,V,H
6	Bacillaria paradoxa Gmel.	11398.100	M,V

Appendix A. (Continued)

Size class	Taxon	Cell volume (um3)	Location
4	*Biddulphia laevis* (Ehr.) Hust.	1227.180	V
3	*Cocconeis* sp.	495.389	V
3	*C. diminuta* Pant.	425.062	V
4	*C. placentula* var. *euglypta*	6823.850	V
3	*C. placentula* var. *euglypta* (Ehr.) Cleve	1428.320	P,V
2	*Cyclotella* sp.	301.593	H
3	*C.* sp.	1200.000	M
1	*C. atomus* Hust.	63.617	P,M,V,H
2	*C. atomus*	220.893	P,H
4	*C. bodanica* var. *michiganensis* Skv.	11858.00	P,M
1	*C. glomerata* Bachm.	64.000	M
2	*C. glomerata*	215.372	V,H
1	*C. meneghiniana* Kg.	63.617	P,M,H
2	*C. meneghiniana*	224.357	P,M,V,H
3	*C. meneghiniana*	1282.950	P,M,V,H
1	*C. michiganiana* Skv.	65.000	P,M
2	*C. michiganiana*	567.057	P,M,H
3	*C. michiganiana*	1847.260	P,M
1	*C. ocellata* Pant.	63.617	P
2	*C. ocellata*	187.035	P
3	*C. ocellata*	1460.060	P
1	*C. pseudostelligera* Hust.	65.188	P,M,V,H
2	*C. pseudostelligera*	229.729	P,M,V,H
4	*Cymbella affinis* Kutz.	1821.240	P
4	*C. amphicephala* Naeg. ex. Kutz.	822.422	P
3	*C. microcephala* var. *crassa* Reim.	338.540	P
4	*C. cistula* (Ehr.) Kirchn.	1453.590	M
4	*C. pusilla*	124.093	P
4	*C. minuta* Hilse ex. Rabh.	1671.240	V
4	*Diatoma vulgare* Bory.	6500.000	M
5	*D. vulgare*	6568.000	P,V
6	*D. vulgare*	6568.160	V,H
4	*D. vulgare* var. *breve* Grun.	4039.680	P
4	*D. tenue* Ag.	196.350	V
6	*D. tenue* var. *elongatum* Lyngb.	445.321	V
3	*Eunotia* sp.	159.174	V
6	*Fragilaria crotonensis* (Edw.) Kitt.	1037.960	P,M,V,H
3	*F. leptostauron* (Ehr.) Hust.	196.350	V
4	*F. vaucheriae* (Kutz.) Peters	104.720	P
6	*F. vaucheriae*	117.810	P
4	*Gomphonema* sp.	741.372	P,M,H
6	*G. intracatum* Kutz.	5268.320	M
3	*G. parvulum* Levis	29.688	P,V
6	*Gyrosigma* sp.	3997.590	M,V,H

Appendix A. (Continued)

Size class	Taxon	Cell volume (um3)	Location
6	Gyrosigma spenserii var. curvula (Grun.) Reim.	6795.300	P
4	Mastologloia smithii Thwaites ex. W. Smith	2686.860	P
6	Melosira granulata (Ehr.) Ralfs	500.000	P
6	M. granulata var. angustissima O. M.	551.855	P,M,V,H
6	M. varians Ag.	6698.060	M,V,H
4	Navicula sp.	589.049	P,M
4	N. cryptocephala var. minuta Boye-P.	632.879	V
3	N. longirostris Hust.	150.999	P
3	Navicula pupula Kutz.	441.372	P
3	N. pygmaea Kutz.	321.372	P,V,H
4	N. radiosa var. tenella (Breb. ex. Kutz.) Grun.	1424.190	M,V,H
4	N. tripunctata (Mull.) Bory.	911.847	P,M,V
3	Nitzschia sp.	156.206	M,V
4	N. sp.	234.147	P,M,V,H
4	N. accedans Hust.	376.991	M
5	N. acicularis W. Smith	54.454	P,V
6	N. acicularis	218.561	V
6	N. acicularis var. closteroides Grun.	207.345	P
5	N. denticula Grun.	2361.810	P
6	N. denticula	5667.290	P,M
4	N. dissipata (Kutz.) Grun.	338.265	P,V
5	N. gracilis Hantzsch.	210.280	M,V
6	N. gracilis	523.468	M
4	N. kutzingiana Hilse	104.720	P,M
1	N. frustulum var. perpusilla (Rabh.) Grun.	23.562	P
3	N. microcephala Grun.	88.357	M
4	N. palea (Kutz.) W. Smith	1281.370	P,M,V,H
5	N. palea	113.425	P,M
6	N. acuta Hantzsch.	3820.180	V
4	Rhizosolenia eriensis var. morsa W. and G. S. West	64.523	V,H
5	R. eriensis var. morsa	65.450	P,M,V,H
4	R. eriensis var. brevispina Wol.	65.450	P
5	R. eriensis var. brevispina	65.450	H
4	Rhoicosphenia curvata (Kutz.) Grun.	717.423	P,V
6	Stenopterobia pelagica Hust.	24077.400	P,M,V
2	Stephanodiscus astraea (Ehr.) Grun.	1130.970	V,H
3	S. astraea	3326.850	V,H

Appendix A. (Continued)

Size class	Taxon	Cell volume (um3)	Location
4	S. astraea	6232.130	P,M,H
2	S. astraea var. minutula (Kg.) Grun.	287.161	P
3	S. astraea var. minutula	2814.870	P,M
3	S. hantzschii Grun.	929.388	V
4	Synedra sp.	336.739	M
5	S. sp.	481.056	V
6	S. sp.	400.000	P,M,V
4	S. filiformis var. exilis ? Cl.-Eul.	53.014	P
6	S. filiformis var. exilis ?	368.155	M
6	S. affinis Kutz. in sensu Hust.	1066.960	M
6	S. acus Kutz.	980.177	M
6	S. delicatissima W. Smith	471.239	V,H
6	S. delicatissima var. angustissima Grun.	359.974	P,M,V,H
4	S. radians Kutz.	311.104	P,V,H
5	S. radians	330.000	P,M
6	S. radians	355.444	P,V,H
6	S. ulna (Nitz.) Ehr.	22048.000	P,M,V,H
4	S. minuscula Grun.	287.450	M
3	Unidentified Pennale	358.540	V,H
	CYANOPHYTA		
6	Anabaena sp.	*500.000	P,M,V,H
6	A. affinis Lemmermann	*245.437	P
6	A. minderi Huber-Pestalozzi	*479.800	P,M,V,H
4	Anabaenopsis sp.	*500.000	P
4	A. circularis (G. S. West) Wolsz. and Miller	*500.000	P
5	A. elenkinii Miller	*527.700	P,M,V,H
4	A. tanganykae (G. S. West) Wolosz. and Miller	*209.603	H
6	Aphanocapsa sp.	33.510	P,M,H
4	A. elachista var. conferta West and West	28.731	M
6	A. rivularis (Carm.) Rabh.	99.541	M
4	Chroococcus limneticus Lemm.	220.900	P,M,V,H
5	C. limneticus	243.727	P,M,H
4	C. prescottii Drouet and Drouet	98.175	P,M,H
6	Coelosphaerium dubium Grunow	30.000	P,M
6	C. naegelianum Unger	33.510	M,V,H
6	C. pallidum Lemm.	4.241	M
3	Dactylococcopsis irregularis G. M. Smith	9.459	P,V,H

Appendix A. (Continued)

Size class	Taxon	Cell volume (um3)	Location
4	D. irregularis	12.837	P,M,V,H
3	Gomphosphaeria lacustris Chodat	8.181	P,M
3	G. lacustris var. compacta Lemm.	14.137	P
6	Lyngbya birgei G. M. Smith	*215573.000	M,V,H
2	Merismopedia sp.	25.000	P
2	M. punctata Meyen	50.000	H
2	M. minima Beck	0.113	P,V,H
4	M. minima	0.113	M
4	M. tenuissima Lemm.	9.630	M
6	Microcystis aeruginosa Kuetz. emend. Elenkin.	65.450	P,M,V,H
6	Oscillatoria sp.	*8523.140	P,M,V,H
6	O. agardhii Gomont	*8782.850	P,V,H
6	O. bornetii ? Zukel	*338467.000	P
6	O. limnetica Lemm.	*90.779	P,M,V,H
6	O. tenuis Agardh.	*14179.200	M,V,H
6	Pseudoanabaena sp.	*392.699	P
6	Raphidiopsis curvata Fritsch and Rich	*224.503	P,M,V,H
6	Spirulina laxissima G. S. West	*500.000	H
6	S. major Kutz.	*526.256	P,M,V,H
6	S. subsalsa Oersted	*654.498	P,V,H
	CHLOROMONODOPHYTA		
3	Gonyostomum sp.	1047.200	M
5	Gonyostomum semen (Ehr.) Diesing	536.689	H
	UNIDENTIFIED FLAGELLATES		
1	microflagellates (<5 um)	8.181	P,M,V,H
2	flagellates (5.1-11.0 um)	220.893	P,M,V,H
3	flagellates (11.1-20.9 um)	904.779	P,M,V,H
4	flagellates (21-44.9 um)	8181.230	H
5	flagellates (45-63.9 um)	16362.500	V